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THE HEMLOCK BORER, ITS BIOLOGY, AND A DISCUSSION OF THE FACTORS CONCERNED IN THE DEVELOPMENT OF AN INFESTATION

A Detailed Report on the Hemlock Borer Investigation
Conducted on the Menominee Indian Reservation during 1937-41.

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THE HEMLOCK BORER, ITS BIOLOGY, AND A DISCUSSION OF THE FACTORS CONCERNED IN THE DEVELOPMENT OF AN INFESTATION

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From time to time since the beginning of this century, extensive killing of eastern hemlock (Tsuga canadensis Carriere) by the hemlock borer, Melanophila fulvoguttata (Harr.), has been reported. As early as 1902 Hopkins (23) stated, "The Eastern Hemlock has a serious enemy in the hemlock destroyer (Melanophila fulvoguttata), which has caused the death of a large amount of hemlock timber throughout the Appalachian and Northeastern regions." The observations of Blackman and Ellis (2) in the Adirondack forests indicated that under forest conditions this insect showed characteristics of being secondary. However, they stated that in more thickly settled regions, where the timber had been largely cut out so as to form open groves, the borer often did a considerable amount of damage. Uncertainty as to whether it should be considered primary under certain conditions has prevailed until the present time.

In 1936 the hemlock borer was reported to be in epidemic form on the Menominee Indian Reservation, Wisconsin, and to be responsible apparently for the death of a considerable volume of hemlock timber (fig. 1).

1/ The studies on which this bulletin is based were made possible through the cooperation of Richard P. Delaney, Assistant Regional Forester (Forest Supervisor of the Menominee Indian Reservation, 1935-40), of the Indian Service, and the Indian Division of the Civilian Conservation Corps, U. S. Department of the Interior.

Heritage (21) estimated that by 1938 the loss was not less than 135 million board feet of timber killed during the previous 5 years. Smaller infestations were also reported on the Nicolet and Chequamegon National Forests and on timberlands of certain private lumber companies of Wisconsin and Upper Michigan. The hemlock borer infestation was considered one of the major forest insect problems of the Lake States Region, since over nine billion board feet, or about one half the total softwood sawtimber volume in the region, is hemlock.

A review of literature revealed little published information regarding the habits of this insect. The publications by Blackman and Ellis (2) and Blackman and Stage (3) have been the source for most of the information obtained. In recent literature there are conflicting statements regarding the length of the life cycle and other minor points. For example, Felt and Rankin (15) state that the life cycle is probably 2 years, while Herrick (22) says it occupies 1 year.

An investigation was undertaken in 1937 at the Menominee Indian Reservation by the Bureau of Entomology and Plant Quarantine to study the habits of the hemlock borer, to ascertain if it should be considered primary or secondary, and to determine if control measures were necessary or practical.[2/] A minor phase of this major project was to clear up the various points of differences in the life history and habits.

2/ The author gratefully acknowledges the work of L. E. Yeager, formerly of the Bureau of Entomology and Plant Quarantine, who conducted the investigation in 1937.

HOSTS AND DISTRIBUTION

No attempt was made to determine the hosts since Blackman and Stage (3) had made a detailed study of this phase. They bred this insect from hemlock, red spruce, and larch.

The hemlock borer is found in the United States throughout the range of the eastern hemlock, which is from the Lake States east to and including the New England States, the North Atlantic States, and south along the Appalachian Mountains into northern Georgia and Alabama. Leng (25) lists this borer as reported from Canada, Labrador, Alaska, and Siberia.

LIFE HISTORY AND HABITS

Description of the adult and immature stages

The beetle is of typical buprestid shape, with a flattened and black metallic colored body. Although specimens measuring 7 to 13 mm. in length have been taken, the average length is 10 mm. The average width at the widest point of the elytra, or wing covers, just posterior of their base is 4 mm. Each wing cover is commonly, though not necessarily, marked with 1 to 4 yellowish- or orange-colored spots. The most prevalent spotting pattern is 3 spots per wing cover. An examination of 1200 beetles collected in June 1939 showed that 37 percent had no spots, 25 percent had faint spots, and 38 percent had prominent spots. About 65 percent of the "spotted" beetles had 3 spots on each wing cover, with the remainder about equally divided between 1 spot and 2 spots. Although a few of the beetles had 4 spots on each wing cover, these were rare and constituted less than 1 percent of the beetles examined (fig. 2).

As a general rule the larvae are white, but when feeding in discolored cambium areas they sometimes acquire a temporary yellowish or creamy tint. They have the wide second thoracic segment and slender abdomen characteristic of buprestid larvae. As described by Blackman and Ellis (2) the prothorax is marked upon its upper surface by an inverted "V". When mature they are from 20 to 27 mm. long (fig. 3,A).

The eggs are white, soft, and slightly oval in shape, and average 0.85 mm. long and 0.70 mm. wide. During the course of oviposition and attachment to the bark, the egg is frequently somewhat flattened (fig. 3,B). When removed from gravid beetles the eggs are perfectly oval. The masses of primary oocytes resemble pods of grapes.

Incubation period

Actual field observations by the writer showed that under normal conditions the eggs hatch in about a week, with temperature exerting an influence on the length of the incubation period. Cool temperatures may prolong this period several days.

Factors affecting the length of the larval stage

The larval period may vary from 10 to 22 months depending primarily upon the time of oviposition and the condition of the host material. Variations of a few weeks in the length of the larval and pupal stages may be caused by a prolonged period of high or low temperatures during the spring and early summer months.

Time of oviposition.--In suitable host material larvae from early summer (June-July) ovipositions complete their development during the current growing season and overwinter in the bark as mature larvae. They

pupate and emerge the following summer, completing a 1-year life cycle. Larvae from late summer (August) ovipositions overwinter the first year as immature larvae in their feeding galleries in the cambium. Completing their development the next year they enter the bark, usually in August but occasionally in late July. The mature larvae evidently require exposure to winter temperatures before they are capable of pupating. Numerous instances were observed of trees in which the borers had reached maturity and were resting in their bark cells in early August but from which no beetle emergence occurred until the following spring. Winter examinations showed that no pupation occurred before spring. Emergence from these trees took place in the early summer, completing a 2-year life cycle.

Condition of host material.--That there is a relationship between the condition of the host tree and attack by the hemlock borer was indicated by a study which showed that in every case the borers can complete their life cycle only in severely weakened and dying trees. Larvae have been found feeding on both living, white cambium tissue and on dying, recently discolored cambium tissue that was still moist and apparently free of any fermentation. Although they appeared to prefer the former, particularly in the early larval instars, this study showed that half-grown larvae could complete development in cut logs on the latter type of cambium tissue. Drying or excess fermentation of the cambium tissue results in the death of any immature larvae that are present.

Temperature effect.--To determine the effects of temperature on the pupal period and time of beetle emergence, eight infested trees were selected in 1939 and, before larval activity was resumed in the spring, they were felled and cut into logs 16 feet in length. The second and third logs were chosen for this study because the majority of the borer popula-

tion is found in this portion of the trunk. They were decked so that the south quadrant was uppermost in all cases. To make the decks as nearly identical as possible, part of the lower logs were placed in one deck and part in the other. The upper log of each tree was placed in the opposite deck from its lower log. One log from each tree was placed in an open, burned-over area where it would be exposed to full sunlight. The other log was placed in an adjoining area, beneath a dense overstory of mature hemlock where there would be heavy shade and consequently a lower air temperature. The length of the pupal period, and the dates of the initial and peak of the beetle emergence for each log was determined (a) by periodically marking and tallying all new emergence holes, and (b) by periodically removing and examining a square foot of bark from the upper and lower surfaces of each of several logs selected because of their heavy borer population.

The data showed that there may be a difference of 4 to 5 weeks between the peaks of beetle emergence from the upper and lower surfaces of a log if it is in the open (table 1). Similarly, there are frequently differences of 4 weeks between dates of emergence of the first beetles from these surfaces. The peaks of emergence from these same surfaces of logs in the shade had a difference of 2 to 3 weeks with similar differences between dates of initial emergence. Both the initial and peak dates for the upper and lower surfaces of the logs in the shade were 2 to 4 weeks later than those for corresponding surfaces in the open. The practical application, to be gained from this information, is that when it is necessary to leave infested logs in the woods after borer activity is resumed, they should be decked in the shade during the winter or early spring. This will lengthen the developmental period and

Table 1.--Beetle emergence, by dates, from upper and lower surfaces of logs in open and shaded decks

SURFACE of LOG	LOG No.	DECK IN OPEN: MAY 22	MAY 26	JUNE 2	JUNE 9	JUNE 17	JUNE 30	JULY 10	JULY 17	JULY 31	AUGUST 11	AUGUST 22	AUGUST 30
Upper	1B	0	0	0	0	0	0	0	0	1	0	0	0
Lower			0	0	0	0	0	0	0	0	0	0	0
Upper	2A	1	1	0	0	0	1	0	0	0	0	0	0
Lower			0	0	0	0	0	0	0	0	0	0	0
Upper	3B	0	0	0	0	0	0	0	0	0	0	0	0
Lower			0	1*	0	0	5	1	0	3*	0	0	0
Upper	4A	5	6	0	4*	1*	1*	1*	0	0	0	0	0
Lower			0	11*	0	1	1	7	10	8	0	2	0
Upper	5B	0	0	0	0	0	0	0	0	0	0	0	0
Lower			0	0	0	0	0	0	0	0	0	1	0
Upper	6A	0	0	0	0	0	0	0	0	0	0	0	0
Lower			0	0	0	0	0	0	0	0	0	0	0
Upper	7B	6	16	3	4*	4*	0	0	0	0	0	0	0
Lower			2*	0	1	8	14	7	3	2	3	0	0
Upper	8A	4	13	3	8	3	5*	0	0	1*	0	3*	0
Lower			3*	0	0	1	16	27	11	11	0	0	0
TOTAL													
Upper		16	36	6	16	8	7	1	0	2	0	3	0
Lower			5	12	1	10	36	42	24	24	3	3	0

SURFACE of LOG	LOG No.	DECK IN SHADE: MAY 22	MAY 26	JUNE 2	JUNE 9	JUNE 19	JUNE 30	JULY 10	JULY 19	JULY 31	AUGUST 11	AUGUST 22	AUGUST 30
Upper	1A	0	0	0	2	0	4	2	2	4	0	0	0
Lower			0	0	0	0	0	0	4	4	0	0	0
Upper	2B	0	0	0	0	0	0	0	0	0	0	0	0
Lower			0	0	0	0	0	0	0	0	0	0	0
Upper	3A	0	0	0	10	5	21	12	3	1	0	0	0
Lower			0	0	1*	0	0	16	8	5	3	1	2
Upper	4B	0	0	0	5	0	15	13	2	2	0	0	0
Lower			0	0	0	0	0	1	2	5	2	0	3
Upper	5A	0	0	0	1	2	45	15	1	0	1	0	0
Lower			0	0	0	0	0	9	3	3	0	0	0
Upper	6B	0	0	0	0	0	0	0	0	0	0	0	0
Lower			0	0	0	0	0	0	1	0	0	0	0
Upper	7A	0	0	0	1	0	17	4	1	0	0	0	1
Lower			0	0	0	2*	0	2	11	8	1	0	2*
Upper	8B	0	0	0	0	0	3	3	0	0	0	0	0
Lower			0	0	0	0	2	0	1	0	1	0	0
TOTAL													
Upper		0	0	0	19	7	106	49	9	7	1	0	1
Lower			0	0	1	2	2	28	30	25	7	1	8

Underlined sections indicate peaks of emergence.
*Practically all of these beetles emerged from the bark on the sides of the logs.

delay the emergence of the beetles, thereby permitting more time to get the logs into the water before this occurs. Should spring softening of the logging roads, or other conditions, prevent removal of such decks until sometime after resumption of borer activity, the slower development of the borers under dense shade conditions will cause much of the beetle emergence to occur so late in the summer that their progeny will have a 2-year life cycle, thus materially reducing the potential rate of increase of the borer population, and allowing a longer period for salvage operations.

To determine the daily temperature range during the pupation period, the temperatures were recorded at hourly intervals throughout certain sample days. In order to obtain data on maximum differences, clear days were usually selected. Air temperatures were recorded by a hygrothermograph housed in a weather instrument shelter. Air temperatures at the bark surface were measured with mercury thermometers, and subcortical bark temperatures were determined by using a portable potentiometer equipped with a number of thermocouples and a multiple switch. Information to explain the difference in rate of borer development was obtained in this study. In late May on clear days when the daily air temperatures in the shade did not exceed 66° F., the maximum difference in air temperature at the bark surface between the upper and lower surfaces of the logs in the exposed deck was about 48° F., with a daily range between 10:00 a.m. and 4:00 p.m. of 72° to 112° for the upper surfaces and 55° to 64° for the lower surfaces. At the same time there was a similar maximum difference of only 16° F., with a daily range of 57° to 72° for the upper surfaces and 50° to 56° for the lower surfaces of the logs in the shaded deck. During early June max-

imum differences of 75° F. at the bark surface and 38° F. in the subcortical bark were obtained for the upper and lower surfaces of the logs in the open deck. The maximum air temperatures at bark surface and for the subcortical bark of the upper surfaces of these logs were 140° F. and 100° F. respectively. These data suggest that, due to warmer environment, the borers in the bark of the more exposed surfaces completed development and the beetles emerged 4 to 5 weeks earlier than did those in the more protected bark. They had resumed activity earlier and had developed to beetles with greater rapidity.

Although no attempt was made to determine the lethal subcortical temperature for the larvae, there is evidence that they can endure rather high temperatures. Two trees, numbers 2 and 6, were selected for the purpose of studying temperature effects on late 1938 ovipositions. When cut in April 1939 both contained heavy populations of very small larvae, about one-quarter grown. Sample logs of each were placed in the decks previously mentioned. These larvae reached maturity in early August under exposed conditions, but as shown in table 1, no beetles emerged except a few which developed from occasional attacks early in 1938. Living larvae were found in the upper surfaces of both these logs when sampled in August and September. This indicated the high heat tolerance of the larvae, since maximum subcortical temperatures of 110° F. had been measured as early as June 6 when the accompanying air temperature in the shade was 88° F. The maximum air (shade) temperatures for June, July, and August, recorded by a hygrothermograph in a weather instrument shelter a few feet away from the logs, were 88°, 88°, and 90° F. respectively. Thus, subcortical temperatures of

at least 110° F. occurred several times on the upper surfaces of these logs during the summer of 1939, yet the larvae were not killed.

Graham (16) found a subcortical temperature of 120° F. to be lethal for hemlock borer larvae in logs. During the 3 years of his study, 1939 to 1941, the recorded subcortical temperature on the sunny side of exposed standing trees never reached a maximum, even on the southwest quadrant, of over 110° F. "Therefore", he concluded, "it seems logical to assume that temperature conditions in the standing trees during the growing season seldom, if ever, fall outside the zone of effective temperature for the borer."

The temperatures on the log surfaces were much higher. For example, a subcortical temperature of 100° F. was usually accompanied by a bark surface temperature of 130° to 140° F. The logs from trees No. 2 and 6 were 18 to 20 inches in diameter, had a total phloem and bark thickness of about 1 inch, and were laid in a north-south direction. In the same area some windthrown trees of 10-inch diameter, with a total phloem and bark thickness of about a half-inch, were laid in an east-west direction. In contrast to the larval survival in the larger logs these smaller trees had practically a total killing of the borers in the upper, south quadrant of their trunks. These data indicate that, although tree bark acts principally as protection against moisture loss and offers little protection against heat, perhaps in this case the maximum subcortical temperatures were so near the critical zone between lethal and non-lethal temperatures, that the difference in the orientation of the logs and the greater thickness of the phloem and bark layers of the larger logs gave sufficient additional protection so that the larvae in their upper quadrants survived while those in the south quadrant of the

smaller trees were killed.

Craighead (9) has shown that certain wood borers in ash logs were killed by solar heat when the logs were exposed to direct sunlight. This method has also been effectively used to control the mountain pine beetle in lodgepole pine (33). The log deck study showed, however, that in hemlock logs of the usual sawtimber size (about 18" diameter) effective control of the hemlock borer cannot be obtained by this method.

Pupal period

The usual length of the pupal period varies from 4 to 6 weeks. This variation may be caused by certain environmental factors, particularly temperature. During the course of studying the relation of temperature to the time of beetle emergence from logs of the exposed and shaded decks, it appeared that temperature differences lengthened the pupal period. The period for borers in the bark of the upper surfaces of logs cut and decked in the open during the winter months was about 4 weeks with much of the beetle emergence occurring the last week in May. The pupal period for borers of the upper surfaces of logs cut in May in most cases was reduced to 3 weeks when decked in open areas and subjected to June temperatures. The usual pupal period was 5 to 6 weeks for borers in the bark of the lower surfaces of logs of exposed decks and the upper surfaces of the logs of shaded decks. Pupation under these more protected conditions did not commence until some time after it occurred in the upper surfaces of the logs of the exposed decks. Thus, beetle emergence did not reach its peak until the last of June. The pupal period in the bark of the lower surfaces of the logs in the shaded deck was longer and specific instances of an 8-week period were observed.

Length of life of the beetles

Field collected beetles and beetles removed from caged infested bark immediately after they emerged were observed to determine the maximum length of adult life. The beetles were placed in cages and were supplied with moisture by means of a gauze wick which extended through the cage, and with bark bearing the type of moss on which feeding had been observed. Under laboratory conditions the maximum time any of these beetles remained alive was 10 days. A maximum of 19 days was recorded for beetles in a large cage placed in the woods under dense shade, and partially sheltered from rain by an improvised roof. This indicated that the probable life of "free" beetles is one to two weeks.

Beetle flight period

The beetle flight on the reservation normally begins about June 1 and extends through August. The peak of the beetle emergence in the more open stands occurs in June, but in very dense stands it occurs in July. The earliest beetle flight observed was in 1939 when 16 beetles emerged between May 18 and 22. That year, the beetles were numerous in the open stands on May 29. The latest that beetles have been collected in the field was August 27. Occasional emergences have occurred, however, between August 22 and 30, so it is probable that some beetles may still be alive as late as the first week of September.

Adult feeding habits

From time to time beetles were observed in the field feeding on a moss, Dicranum montanum Hedw., which grows in abundance on the bark of hemlock trunks. Two green trees were felled in a heavily infested stand and observations made to determine if the beetles fed on the foliage. Although the beetles were quite abundant, and many were crawling about

on the felled trees, none were observed to feed either on the old or new needles of the foliage. Under cage conditions, however, they fed to a limited extent on the new needles, but appeared to prefer the moss which was also available.

Oviposition habits

A period of about 3 days is required following emergence of the females before the eggs begin to mature. When newly emerged females, which had not been confined in cages for more than 2 days following emergence, were dissected there were no mature eggs but the primary oocytes were found in clusters and were rather colorless, semi-transparent, and difficult to separate and count. When mature the eggs are white, can be seen with the naked eye, and are relatively easy to separate and count. Copulation and feeding were observed during the period of maturation of the eggs.

When ovipositing the female crawls about on the trunk inserting her ovipositor in various crevices in the bark, apparently seeking one of satisfactory depth and width. When one has been located, there is usually a pause of about 20 seconds while the egg is laid. With a little practice it is possible, by simply observing the beetles, to determine with accuracy when an egg is laid. The favorite place for ovipositing is beneath loose flakes of bark, and the eggs are usually laid singly, although it is not unusual to find 2 or even 3 eggs together. Instances of as many as 8 eggs in a single mass have been found, but it is not known whether these were laid by one beetle or by several which chanced to choose the same crevice. The duration of the egg-laying period for an individual was not determined, but it is known to last at least several days.

Tropic responses of ovipositing beetles

The behavior of ovipositing beetles is controlled by certain tropisms, chiefly those relating to temperature and light. There is a very definite relation between the air temperature in the shade and the daily migration of the beetles to the trees, this temperature being between 70° and 75° F. On rainy days or unusually cool, cloudy days the beetles are inactive and the females do not lay eggs. In a study carried out in 1939 it was found that 80 percent of the oviposition occurred when the air temperature at the bark surface was between 82° and 92° F. The range was 75° to 95° with the optimum at about 86°. That there is a phototropic response was indicated by the fact that the majority of the eggs were deposited on that part of the tree trunk which was exposed to the sun at the time of oviposition.

Copulation habits

The male beetles are very active during the flight period, continually moving from tree to tree in search of the females. Immediately after copulation the male departs. No instances of repeated copulation between the same pair of beetles, as is common with certain Cerambycids, has been observed. Observations indicate that the females are repeatedly fertilized during the period of maturation and laying of the eggs.

Biotic potential

The probable biotic potential was determined by dissecting about 30 females. Beetles which emerged from caged material were held for 3 to 5 days to permit greater development of the eggs and then were dissected and the eggs and primary oocytes counted. Many of the beetles would have

produced 130 to 160 eggs and practically all of them were within a range of 100 to 160 eggs. Only about one-half of this number were mature at the time of examination. The remainder were about half the size of the mature eggs or were primary oocytes. The abdominal cavities were filled to capacity and it was apparent that there would not be sufficient room for the immature eggs to complete development until a portion of the mature eggs had been deposited. Field collected females, taken while ovipositing and immediately dissected, contained both mature and immature eggs. Dead females found in the field were dissected and found to be spent - thus indicating that all or practically all the eggs had been laid before death.

Sex ratio

The sex of 434 beetles, emerging from caged materials, was determined. Since the last ventral segment of the male tapers to a blunter point than that of the female and is usually notched, the sex could easily be determined with the aid of a hand lens. Of these 484 beetles, 225 were males and 259 were females - approximately a 1 to 1 ratio.

Sex ratio of the daily migration to the trees

In 2 days of field collecting by a 3-man crew 1200 beetles were taken, and were caged according to the hour of the day they were collected. A tally showed no great difference in the sex ratio for the entire day. This agreed with counts of caged material which had indicated a sex ratio of approximately one to one. However, on moderately cool days during the first hour or two of collecting, the number of males frequently exceeded the number of females by about 20 percent. In the late forenoon collections

the sexes were about equal. The afternoon collections, when the temperatures were high, usually contained a decidedly greater number of females. This was probably because the males were more active and more difficult to collect and not because of any change in the sex ratio.

INDICATIONS OF INJURY AND CHARACTER OF DAMAGE

Woodpecker work

When present, woodpecker work on the boles of the trees is the most noticeable indicator of borer infestation. However, this is of little value in salvage operations since the birds do not normally commence working on the trees until the borers are mature and have tunneled into the bark. By this time the trees are either dead or definitely dying and their foliage is so obviously thin that they can easily be detected by this character alone - even if woodpecker work is not present. The woodpeckers chip the outer bark from the trees in their search for borers. In some instances a third or more of the outer bark had been removed from heavily infested trees during the course of a winter's feeding, and the exposed reddish inner bark made these trees very noticeable.

Root rotting fungi

The shoestring fungus, Armillaria mellea (Vahl.) Quel., was found on all trees having successful borer attacks. Its presence was indicated by wet, black soot-like spots on the bark of the tree just above ground level, the sporophores which are present in September, the mycelial fans which stream upward from the roots between the phloem and xylem, and black rhizomorphs or "shoestrings" in the soil and litter of the forest floor. The sporophores, figure 4, are soft-bodied mushrooms which decay so rapidly

that usually even their remains are difficult to locate a few weeks after the spores have been liberated. The black rhizomorphs do not necessarily indicate that the trees near which they are found are infected since this rot is ubiquitous and attacks and develops on the decaying organic material of the litter. Cankers were common on both the main and small roots of the drought-injured hemlocks. They frequently failed to callous over on the roots of weak and dying trees and some of the roots were eventually severed (fig. 5).

Crown and stem characters

The forestry department of the Menominee Indian Reservation had urgent need of a method for detecting the trees which were in the early stages of successful borer attack or were in such a weakened condition that although not infested at the time they were definitely dying and would soon be brood trees. Such information would permit more efficient marking and would lengthen the cutting cycle for salvage operations. In the late summer of 1938 during the course of examining the permanent sample plots established in 1937 and 1938 (discussed in detail later in this report), it became increasingly apparent that certain crown and stem characteristics had a relation to growth and borer attack. In 1939 additional study showed that it would be possible to select trees which would die within 2 years. These characteristics were: (1) thinning of the foliage, particularly at the terminal portions of the branches in the upper third of the crown; (2) wet, black, soot-like spots on the bark just above ground level; (3) narrow annual rings followed by the total absence of any wood laid on at the base of the tree for the last 2 years, or by a partial ring for the first of these 2 years; (4) the presence of numerous unsuccessful borer attack gal-

leries in the cambium tissues; (5) yellowish-green foliage, which usually became noticeable from 3 to 10 months before complete shattering of the needles. The third and fourth characteristics were used merely to verify the suspicions raised by the first and second, and when the fifth characteristic was very pronounced it indicated that the tree was dead.

The decadence of hemlock is usually first indicated by the thinning of the foliage, particularly at the terminal portions of the branches in the upper crown. This can be detected by an experienced marking crew at least 2 years prior to complete needle fall. Tree 45, figure 6, shows the crown condition of a tree having heavy unsuccessful borer attack. The advanced thinning of the branch terminals of this tree indicates that it will be practically bare within a year. The crown of the tree at the left shows that it has suffered light injury from the drought but it will recover. Three hemlocks with crowns that are typical of a vigorous healthy tree, a dying tree and a dead tree are shown by figure 7.

These 5 characteristics were pointed out to the supervisor of the reservation who, after repeated checking, was so convinced of their value that he incorporated them in his marking system. Using them, a 40-acre area was marked for cutting in the fall of 1939 and the marking crew was instructed in the technique of choosing the trees. This area was examined in 1940 and again in 1941 and no dying trees were apparent.

At this time, the pulp mill, which obtained its supply from the reservation, would accept hemlock logs that did not have more than 1½ inch of sap rot. This amount of sap rot normally does not develop within the first 3 years following complete needle fall. Thus, since dying trees could now be detected 2 years prior to complete needle fall, it was possible

to lengthen the salvage operations from a 3-year to a 5-year cycle.

Character of the injury by the borer

In a "successful attack" the gallery is about 9 to 11 inches long. For the first 1 or 2 inches it extends as a slightly winding gallery from the point of oviposition in the crevice at the surface of the bark through the bark and phloem tissues to the cambium layer. The larva then feeds on the cambium between the phloem and the xylem, making a meandering gallery which is 6 to 8 inches long by the time it completes feeding and developing. As it grows it requires a gallery of greater diameter and chips out more and more of the phloem and xylem tissues on either side of the cambium. This gallery is about half in the phloem and half in the xylem. When a larva becomes full-grown it re-enters the bark, making a sloping gallery from 1 to 1½ inches in length. Just beneath the outer bark it constructs its pupal cell.

In successful attacks the larvae have completed feeding and burrowed into the bark, from which they have either emerged as adults or are still present in the pupal cells preparatory to emerging. In advanced unsuccessful attacks the galleries etch the surface of the wood for 3 inches or more, but are never completed because of the premature death of the larvae. In initial unsuccessful attacks the galleries are usually confined to the phloem tissue, but if they do extend to the wood, they etch the surface for less than 3 inches, owing to the early death of the larvae.

After pupation the adult liberates itself by cutting an oval hole through the thin layer of bark covering the outer end of the pupal cell.

The principal damage to the trees is caused by the larvae while in the cambium feeding stage. When present in numbers, the meandering galleries cause a girdling of the cambium tissue of the tree trunk (fig. 3), thereby hastening death.

HOST RESISTANCE AND SUSCEPTIBILITY TO ATTACK

Resistance of trees to controlled attacks

In order to determine resistance to attack periodic examinations were made of 27 trees consisting of 9 groups of 3 trees each. Care was taken in setting up this experiment to select vigorous, thrifty trees that were apparently free of borers and to have the trees in each group as nearly identical as possible. In June 1938 one tree of each group was felled, a second was left as a check, and the third was treated so that half of the stem was girdled at a height of 2 feet above the ground (fig. 9). To assure oviposition, a section of the trunk was caged and in the latter part of June 30 beetles, 20 females and 10 males, were placed therein. In 1939, since the previous season's attacks on the check and half-girdled trees were not successful, the trees were again infested at the rate of 30 females and 20 males per cage. On the felled trees, beetle emergence from the lower boles began in July 1939, completing a 1-year life cycle.

One year after treatment, an examination was made by barking several of the trees. This showed all attacks on the half-girdled trees to be unsuccessful. Most of the galleries were less than a half-inch in length, but a few larvae had succeeded in tunneling in the outer phloem for an inch or two before they were killed by the natural resistance of the trees. However, none of the attacks had succeeded in reaching the cam-

bium. On the check trees, there were no successful attacks and in the unsuccessful attacks no larvae had succeeded in even scarring the phloem.

At the close of the 1940 growing season an examination showed that no beetles had emerged from either the half-girdled or check trees. This indicated that even after being half-girdled for a year the former trees were still not weakened sufficiently to permit successful 1939 attacks. During 1940, several of the trees were successfully attacked for the first time. Noticeable thinning of the foliage indicated that these trees were decadent. During the summer of 1941, there was beetle emergence from these trees followed by complete shattering of the needles. More of the half-girdled trees were now sufficiently decadent to be attacked, and by October the majority were "dead" or "definitely dying"; the remaining half-girdled trees were doomed to die within another 2 years. Increment cores, taken from several quadrants of each of the dead trees, showed that in every case the last complete annual ring on the lower part of the bole was laid on during the growing season, 2 and sometimes 3 years prior to the complete shattering of the needles. Study of these cores showed that usually each dead tree had laid on a complete ring at its base the first summer following girdling, a partial ring the second summer, and none the summer before complete needle-fall occurred. Successful attack by the borer had not occurred until the summer that no wood was laid on the lower bole.

One of the trees that was "definitely dying" in 1940 had laid on partial rings at its base in both 1939 and 1940, and no wood in 1941. When examined in October 1941 it contained small, living larvae, showing that it was apparently being successfully attacked for the first time that year. In 1940 only a few attacks had scarred the phloem and all had been unsuccessful. Although it still retained 75 percent of its foliage

and the foliage color was still normal, barking of the lateral roots at soil level showed the root system to be entirely dead, and mycelial fans of Armillaria mellea were present on most of the main lateral roots. The advanced development of the infection showed that it had been present prior to successful borer attack (fig. 10).

The same was true of the two trees classified as "definitely dying" in October 1941. Both had failed to lay on any wood in 1941 and had been successfully attacked for the first time during that summer. Although these trees still retained 65 to 75 percent of their foliage and the foliage color was still normal, an examination of the main lateral roots showed all to be dead and indicated that the entire root systems were dead. Mycelial fans of Armillaria mellea were present on most of the main roots. Black soot-like spots on the bark near the ground level, and in one instance sporophores, showed that the infection had been present at least one year. Increment cores from breast height indicated the gradual decline in vigor prior to successful borer attack. Both trees laid on complete rings in 1938. In 1939 one tree put on a very narrow complete ring and the other tree put on a partial ring. Both trees put on partial rings in 1940 and none in 1941. Thus, although they retained the major portion of their foliage and the cambium tissues of their trunks were living, practically all of each root system was dead when the trees were first successfully attacked. This fact was brought out most emphatically in the root condition study, to be discussed later, in which the root systems of 30 trees were washed out and carefully examined.

When it was ascertained that successful attack had not occurred on the half-girdled trees, six more trees, having an average diameter breast

high of 24.5 inches, were selected in May 1939 and 90 to 95 percent of their stems girdled at a height of 2 feet above ground. By the fall of 1940 the 95 percent girdled tree had lost all its needles but there was no beetle emergence until the summer of 1941. The other 5 trees, 90 to 92 percent girdled, had noticeably thin foliage and mycelial fans on the main roots in the fall of 1940, but complete shattering of the needles did not occur until the summer of 1941. No beetles emerged from these trees in 1941. Thus, even in these more rapidly dying trees decadence was not sufficient to permit successful attack until so late in 1940 that none of the beetles would emerge until 1942. Increment cores from these trees showed a partial ring on the lower bole in 1939 and none in 1940. Four trees that were completely girdled in July 1939 died within one year.

The series of stem-girdled trees gave evidence of the wide range in the number of years that hemlock trees may live after severe injury. The fact that some of the half-girdled trees will not lose all their foliage until 1942 or 1943, four or five summers after they were treated, explains why the tree mortality from the 1930-37 drought injury continued very noticeably for 2 years after the close of the 1937 growing season. Even the more seriously injured ones, such as those 90 percent girdled, did not lose all of their needles until 2 years after treatment. This lag in tree mortality explains why, at the close of the 1933 season, Forest Supervisor Grapp (17) reported 50 million board feet of hemlock killed on the reservation in the last three years, an average of 17 million feet per year, while in 1939 Heritage (21) reported at least 135 million board feet killed in the preceding 5 years (1934-38), an average of 27 million feet per year.

To obtain further information regarding how long hemlock trees with dead root systems will retain their foliage, six apparently healthy trees were selected in August 1939 and the soil washed from around the root collars of four to a depth of 1 to 2 feet below the collars. All of the roots of two trees were girdled just below the root collars. On two other trees, all but two of the larger roots or about 90 percent of the roots were girdled. One tree of each treatment was girdled by peeling all of the cambium from an area 4 to 6 inches wide on each root (fig. 11). On the remaining tree of each treatment, a similar area was girdled with a blow-torch. Heat was applied until the outer bark was charred and an examination 2 hours after treatment showed the cambium to be discolored and dead. Small dams were built below each tree and soil washed in to the original soil level. The two untreated trees were checks for the four treated trees. On each of the six trees, the bark was peeled from a small area about 4 inches wide and 1 foot long to be certain that all the trees selected were free of borer infestations. The root-girdled trees were attacked by hemlock borer larvae early in the summer of 1940. Figure 12 shows a section of one of the root-girdled trees, indicating that it contained no borer infestation in August 1939 (area A), but it had a population of half-grown larvae by August 1940 (area B), and a population of nearly mature and mature larvae in October 1940 (area C).

Those trees having only 10 percent of their roots functioning held most of their needles until the second growing season following injury. The 100 percent root-girdled trees lost their needles about a year after injury. This indicated that hemlock will retain its needles 1 to 2 years after all or practically all of the root system is

dead, and that the hemlock borer has a 1-year life cycle on a tree in this weak condition.

Unsuccessful attack study

During the course of the investigation, considerable data on unsuccessful borer attacks were collected (fig. 13). Records were kept of the few instances found in which trees had apparently recovered after unsuccessful borer attacks that had succeeded in scarring the wood or xylem tissue (fig. 14,A). A few galleries were found in wood laid on as early as 1859 (fig. 14,B), and numerous gallery scars dating back to 1934 and 1935 were found in green trees of the 1933 and 1934 blowdown area. Seventy-seven unsuccessful attack scars were counted on a 16-foot log from a tree cut in the Camp 24 area during 1938. Usually only a very small percentage of the attacking larvae succeed in tunneling deep enough to etch the wood of such trees, therefore the few gallery scars found represent only a very small portion of the actual attack that took place.

This phenomenon of heavy, localized, unsuccessful borer attack immediately following blowdown illustrates the relationship between heavy borer attack and periods causing abnormal decadence in the forest, such as drought, or heavy windstorms which cause blowdowns. The fact that many trees survived heavy attack in 1934 and 1935, and were alive when examined 4 and 5 years later, is additional evidence that this insect is secondary rather than primary. The presence of galleries dating back to 1859 and 1902 indicated that the hemlock borer had been present on the reservation for a long time, but was not able to develop to a large population until severe drought made conditions favorable.

Root condition study

Conclusive evidence of the primary influence of tree condition on borer development was obtained by a study of the roots of trees having various stages of borer attack. To determine if the hemlock borer should be considered as primary or secondary under forest conditions, the root systems of 16 trees in a virgin stand in the hemlock type were washed out and examined during the summer of 1939 (fig. 15).

Blackman and Ellis (2, page 50) in discussing thinned hemlock stands state, "In these cases it is a question whether the openness of the stand so weakens the remaining trees as to make them susceptible to the attack of this insect, or whether the scarcity of broken or dying hemlocks compels the beetles to breed in healthy trees. However, the fact remains that hemlocks in the open and in areas which have been over-thinned, are more subject to attack than those occurring under more natural conditions."

In 1940 a study was made of trees in very open stands produced by old blowdowns and logging, to obtain information on the nature of attacks by the borer under stand conditions of this type. The root systems of 14 trees were washed out, and detailed records taken for 12 of them.

The procedure followed in washing out the roots of these trees (fig. 16), and the examination of the roots themselves in both 1939 and 1940 is described in a paper on the causes of decadence of hemlock at the Menominee Indian Reservation by Secrest, MacAloney, and Boyce (35). The trees selected for examination were grouped in three classes, according to the stage of borer attack - successful, unsuccessful, and none or practically no attack. In selecting [illegible] for deter-

mining the probable presence of borers by noting the condition of the tree crown. The presence of the borers was then verified by barking the lower trunk.

As an indicator of the size of the main lateral root system, and to determine what percentage of the main root system was examined, the total number of lateral roots having a diameter of at least 2.5 inches 3 feet from the stump was recorded. As a representative sample 10 to 12 of these roots were selected at approximately equal distances around the circumference of the stump, and these were carefully examined to determine the condition of the root system. At intervals of 3 feet throughout the length of each root the bark was peeled away completely around the circumference and the cambium examined. The condition of each root branching from the main lateral was determined and the percentage which it represented was estimated. From these data the percentage of living root system was calculated. The feeding roots were also carefully examined and the percentage of dead rootcaps and rootlets determined for sample trees in each borer attack class (fig. 17).

Cross-section disks for stem analysis were taken at intervals of 17 feet throughout the length of the trunk of each tree. These gave information regarding the general trend of the growth rate of the various trees during the past 30 years and the dropping out of annual rings on the lower bole prior to successful attack.

Bark samples were taken just above the cross-section disks, at 4 to 6 different heights on the tree trunk corresponding to the basal 4 to 6 disks. A strip of bark about 1 foot wide and the circumference of the tree in length was peeled from each sample height. The area of the bark sample was measured and the number of borers and unsuccessful attacks

recorded according to the stage of development.

A complete account of the root examination work done in 1939 was published in the Journal of Forestry in January 1941. The borer attacks from eggs laid during the preceding summer were found to have been successful only on trees having 10 percent or less of their root systems alive when examined in July 1939. Trees which had been attacked for the first time with apparent success early in the summer of 1939 had 37 to 49 percent of their main lateral roots still alive but with relatively few living root tips. Galleries of unsuccessful attacks were prevalent, but no galleries of successful attack were found in trees having 60 to 80 percent of their main lateral root systems alive and a still smaller percent of living root tips. Trees having 99 to 100 percent of their main lateral root systems alive were classed as check trees. These sometimes had a few galleries of unsuccessful attacks but no galleries of successful attack. It was apparent that hemlock borer attacks could not be successful until the trees were in a dying condition. Therefore, it was concluded that under forest conditions the insect should be considered as secondary.

Active infection by the shoestring fungus was found on all trees having successful borer attack, and it was evident that this fungus should be considered only a secondary factor in the death of the trees under forest conditions. The advanced stage of infection in many cases indicated that fungus was present prior to the initiation of successful borer attack. This was an additional indicator of the secondary nature of the hemlock borer injury.

The shoestring fungus, Armillaria mellea (Vahl.) Quel., is considered by most investigators to be a secondary fungus. Day (11,12) con-

cluded from his studies that this fungus is parasitic only when the vigor of the host has been reduced by unfavorable environmental conditions acting alone or in conjunction with other agencies such as defoliating insects or mildew. Boyce (5) reviews the results obtained by a number of investigators studying this disease. Practically all of their investigations indicated that it is a secondary fungus.

In most of the virgin forest of the Menominee Indian Reservation there is a heavy layer of leaf litter and organic material. In several areas examined, the rhizomorphs were so prevalent throughout this layer of decaying organic material that practically every tree was exposed to infection, yet only a small portion of them were dying. Thus, if this disease were primary under forest conditions practically every tree in these areas would have been infected and dying. Instead, only the more severely drought-injured trees were infected, clearly indicating the secondary nature of the fungus. Therefore, it was concluded that under forest conditions this fungus should be considered only a secondary factor in the death of eastern hemlock (35). Stickel (38), in his study of drought injury in hemlock-hardwood stands in southern Connecticut, found this fungus on many of the trees, both hardwoods and softwoods. He, too, concluded that in all probability the disease was secondary.

The 1940 study in open stand conditions showed successful attack on trees with only 33 to 52 percent of their main laterals alive (table 2). These trees had practically no living root caps and only 2 to 10 percent of the small feeder rootlets had living cambium. They frequently had a larger percentage of their main lateral root systems alive than the 10 percent or

less that had been found for trees in a similar stage of borer attack under virgin forest conditions. This was due largely to the lack of uniformity in root condition, common in open stands. This lack of uniformity was caused, in most cases, by exposure. For example, tree number 50, had a few 1940 emergence holes (table 3), yet 50 percent of the main lateral root system was alive. This is unusually high for a tree with a population of mature borers. This high percentage was due to the fact that many of the roots on the north half of the tree had only recently commenced to die. Although their terminal rootlets were dead, the cambium of the larger roots were still alive. In contrast, practically all of the main lateral roots on the south and southwest quadrants had been dead for several years. This irregularity in root condition was apparently caused by exposure. This tree was on the south border of a small group of hemlocks, which afforded shade and protection to the roots on the north quadrant. Those on the south, however, were in soil that was bare except for a few widely scattered herbaceous plants. Sap rot extended from the base of the tree to a height of 28 feet on the south quadrant, and most of the galleries were in or bordering this quadrant. Thus, the borer population was confined largely to that portion of the trees that had practically no living roots. A somewhat similar condition existed for tree number 48. This irregularity in root condition is primarily responsible for these trees having a higher percentage of living main lateral roots than did tree number 47, although their borer populations were more mature.

Table 2.--Condition of Roots in a Very Open Stand Produced by Old Blowdowns and Logging

Tree No.	Percentage of main lateral roots alive: At stump	At 3 feet	At 6 feet	At 9 feet	Average for 9-foot radius
	Trees successfully attacked				
47	39	37	29	28	33.25
48	50	45	40	34	42.25
50	58	56	53	42	52.25
	Trees unsuccessfully attacked				
56	77	75	55	38	61.25
51	82	78	58	42	65.00
45	91	91	83	59	81.00
42	100	97	73	63	83.25
52	100	95	72	66	83.25
46	100	100	90	82	93.00
54	100	100	100	93	98.25
	Check trees				
41	100	100	100	95	98.75
55	100	100	100	97	99.25

The unsuccessfully attacked trees, whose wood had been etched by the larvae, had 61 to 83 percent of their main lateral root system alive (table 2) and less than 60 percent of their root tips alive. The two trees with light scarring of the phloem but not etching of the wood (Nos. 46 and 54) had 93 and 98 percent of their main root systems alive, but only 80 percent or less of their root tips were living. In the latter, more vigorous tree the galleries were confined to the outer phloem, and it was definitely apparent at the time of the examination that this tree was recovering. Most of the attacks on the other tree were also confined to the outer phloem, but a few had penetrated the phloem and injured the cambium just enough to form pitch blisters. Although the recovery of this tree is more question-

Table 3.--Average Borer Population per Square Foot of Bark Area in a Very Open Stand Produced by Old Blowdowns and Logging

Tree number	Bark: Number of samples	Bark: Area in square feet	Unsuccessful Attacks (Larvae Dead): Confined to phloem	Just through or penetrating the cambium prior to 1939	Just through or penetrating the cambium in 1939	Pitch Blisters[1]: Small	Pitch Blisters[1]: Medium	Pitch Blisters[1]: Large	Wood Etched: Less than 3 inches prior to 1939	Wood Etched: Less than 3 inches in 1939	Wood Etched: 3 inches or greater prior to 1939	Wood Etched: 3 inches or greater in 1939	Mature galleries with bark cells	Larvae alive when examined: Confined to phloem	Larvae alive when examined: Just through or penetrating the cambium	Larvae alive when examined: Wood Etched: 0 to 2.9 inches	Larvae alive when examined: Wood Etched: 3 to 4.9 inches	Larvae alive when examined: Wood Etched: 5 to 9 inches	Larvae alive when examined: Wood Etched: In bark	Beetle emergence holes
Trees Successfully Attacked																				
47	4	17.1	73.6	10.6	Tr.	2.1	0.6	0.5	0	Tr.	0	0	0	.3	.4	2.1	0	0	0	0
48	5	23.1	103.9	5.0	0	3.5	1.5	1.0	0	0.7	0.3	1.3	1.3	.5	0	1.3	0	0.1	0.1	Tr.
50	5	24.5	82.8	5.5	0.2	0.9	0.9	0.9	0.4	0.7	0.3	0.5	2.1	Tr.	0.2	0.8	0.1	0	0.3	0.1
Trees Unsuccessfully Attacked																				
56	5	16.0	60.0	2.2	0	0.6	0.2	0.1	0.3	0	0.1	0	0	0	0	0	0	0	0	0
51	5	24.9	67.1	3.5	0	0.5	0.1	0.1	0	0.2	0	0.3	0	0	0	0	0	0	0	0
45	5	26.6	25.0	0.1	0	1.8	0.6	0.4	0.2	0	0.2	0	0	0	0	0	0	0	0	0
42	5	14.3	16.0	1.5	0.3	0.4	0.1	Tr.	0	Tr.	0	0.1	0	0	0	0	0	0	0	0
52	5	24.4	42.0	0.5	0	0	0	0	0	Tr.	0	0	0	0	0	0	0	0	0	0
46	6	19.3	24.7	0	0	0.9	Tr.	0.2	0	0	0	0	0	0	0	0	0	0	0	0
54	5	25.7	16.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Check Trees																				
41	5	15.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	4	11.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[1] "Small" indicates area of blister is less than the size of a dime; "medium" is from a dime to a quarter in size; "large" is bigger than a quarter.

able, there are other instances in which trees sufficiently weakened at the time of borer attack to permit a limited amount of etching recovered.

The 2 check trees had 98 and 99 percent of their main root systems alive and nearly all of their root tips living. Larvae had not succeeded in even scarring the phloem of these trees. The unsuccessfully attacked trees showed that the beetles oviposit upon trees in which the larvae cannot mature as well as on those in which they can. Therefore, it is reasonable to assume that although a certain amount of oviposition occurs on vigorous trees they are not injured because of their thrifty condition.

Root tip examination

Two trees from each attack class were selected and their root tips were intensively examined. As the root system of each tree was exposed, sample root clusters were collected, labeled, wrapped in moist burlap, and laid in a cool place. Roots were removed as needed and the number of living and dead root caps and feeder rootlets counted. All counts were completed within 24 hours after the samples were collected. The condition of each root tip was determined by snapping the tip and observing whether it was alive or dead. When alive the root caps are brittle, their interior is white, non-fibrous, and potatoe-like in texture. Although in washing out the sample root clusters great care was taken never to turn a solid stream of water directly upon them, it was impossible to avoid a certain amount of breakage of the root caps because of their delicate and brittle texture. The term "root tip" is therefore used to refer to counts whose examination basis is either the root cap or, if this is broken, the brown covered non-fibrous portion of the root immediately back of the root cap. The term "rootlets" refers to the fine fibrous roots to which the root tips

are attached.

The percentage of living root tips varied for different soil depths. Sample roots were collected from each tree from at least 2, and in some instances from 4, different depths. In the upper foot of soil, sample root clusters were collected at random from each of the 10 to 12 main laterals selected for the root condition determination. Sample root clusters were also taken from the few vertical roots present. These were usually vertical branches from some of the larger lateral roots since hemlocks do not have a true tap root. These vertical roots seldom extend to a depth of more than 4 to 6 feet (fig. 18). Hemlocks are shallow-rooted trees, and 90 percent or more of the entire root system is in the upper 24 inches of soil. From each tree selected 30 to 40 root clusters were collected and examined. The number of root tips or root caps examined per tree ranged from approximately 1,000 to 2,473.

Trees No. 47 and 50 were examined as representative of successfully attacked trees. Neither tree had any living root caps or feeder rootlets in the upper foot of soil. At a depth of 4 feet they had practically no living root caps and the cambium of only 2 to 10 percent of the rootlets was still alive. For example, tree 47 had only 2 root caps alive of the 90 found at a depth of 4 feet. Most of the root caps had decayed and were missing. An examination of the vertical branches of 3 living lateral roots showed 30 percent of the rootlets at a depth of 4 feet to be alive. These 3 laterals were the healthiest of the 12 main lateral roots examined. Of the others, 7 were dead and 2 nearly dead. Thus, for the tree as a whole, the percentage of living feeder rootlets at a depth of 4 feet averaged about 2 percent. This very low percentage of living rootlets is due to

the fact that all the roots in the upper layers of soil, where most of the root system was located, were dead. Tree No. 50 was in a little better condition, about 10 percent of its rootlets being alive, but it, too, had practically no living root caps. This indicates the advanced stage of decadence of the root systems of the trees which borers can attack successfully. Both the 1939 and 1940 examirations showed that borer attacks are successful only on trees that have relatively few living root tips.

As representatives of unsuccessfully attacked trees, extensive examination was made of the root systems of trees No. 52 and 54. These trees were selected to indicate the upper limits of the root condition range of attacked trees. The successfully attacked trees had indicated the lower limits of the range. Tree No. 52 was a good tree to indicate the probable root condition division line between unsuccessfully attacked trees, in which the galleries scar but do not succeed in penetrating the phloem, and the trees in which some of the galleries do penetrate the phloem and etch the xylem. It had medium scarring of the phloem but only a trace (less than 0.05 gallery per square foot) of etching of the xylem. For this tree the average percentages of living root tips at various soil depths were 7.5 at 6 inches, 75.0 at 1 foot, 74.0 at 2 feet, and 76.0 at 4 feet. These figures are based on an examination of 2,473 root tips.

Tree No. 54 was in the initial stage of unsuccessful attack. It had light scarring of the phloem, but none of the larvae had reached the wood or penetrated the phloem. For this tree the percentages of living root tips at various soil depths were 72 at 6 inches, 91 at 1 foot, and 88 at 4 feet. These figures are based on an examination of 1,585 root tips.

Check trees No. 41 and 55 had no dead main lateral roots and relatively few dead subordinate roots (table 2). Sample root clusters were collected at depths of 6 inches to 1 foot, and 4 feet. The percentages of living root tips at these depths were 31 and 94 respectively for tree No. 41, and 98 for both depths for tree No. 55. The latter was the more vigorous tree. It was making very good growth, had very dense foliage and 75 percent of the root tips at a depth of 4 feet had succulent living caps. The percentage of root caps was smaller for the root tips of the upper soil layers. This is to be expected, however, for the fine thread-like roots of the terminal portions of the lateral root system are more susceptible to breakage and loss of the root caps during the process of excavation than are the short, stockier roots of the vertical root system.

Under open stand conditions there was a significant difference between the percentage of living root tips in the upper 6 inches of soil and those at depths of 2 and 4 feet. The root tip mortality was always highest in the upper 6 inches. This was obviously due to two factors - lack of moisture and in some instances exposure. During the drought period there were periods of a month or more when no rain fell. During these dry periods the upper soil layers, particularly in the very open stands, became very dry and powdery to a depth of 6 inches or more. It has been shown that an adequate moisture supply is essential to root elongation. According to Kramer (24), "When environmental conditions favor rapid transpiration, cessation of root extension for only one or two days would result in death of many, and possibly most plants from dessication." This points out the vital necessity for the rapid and continuous extension of root systems of transpiring plants. Exposure acted in at least two ways. First, the crowns

of the open stand trees were usually open on several or all sides. The more exposed condition of the crowns of these trees favored rapid transpiration and thus caused a more rapid depletion of the moisture supply available to their roots. Second, in some cases the trees were in an environment where the ground surface received direct sunlight for a considerable portion of the day. Tree No. 50 was an excellent example of this condition. Hall (18), in his study of post-logging decadence, found duff temperatures up to 171° F. in open cut-over stands. It is very probable that under these conditions high soil surface temperatures caused a portion of the root mortality found in the upper 6 inches of soil. However, since greater mortality of the root tips of the upper soil layers was also found under conditions where the soil received ample protection and shading from direct sunlight, it appears that lack of moisture and desiccation of the root tips were the primary causes of this condition.

Ring growth study

To obtain a basis for [illegible] in picture of the various trees, a number of [illegible] examined in 1933 on section lines for which survey notes were available, showing the dates when the lines were established and re-surveyed. Strips were chosen from the blazed faces of some of the trees, and five trees were felled. Cross-sections were taken through the blazed faces and at intervals of 16 feet along the boles. Sufficient variation was found in the width of the annual rings of the preceding 40 years to make it easy to find the ring pattern. Unusual ring combinations which were found [illegible] particular. In the case hemlock trees were the unusually [illegible] 1903, 1905, 1914, 1925, 1929, and

1930, together with the very narrow rings of 1904, 1917, 1926, and 1934 (fig. 19). Most trees had narrow rings in 1911, 1922, and 1938. Subsequent studies have shown that trees which were not severely injured by the drought laid on wide annual rings in 1939, 1940, and 1941.

The cross-section disks from the trees of the 1940 root condition study showed that none of the successfully attacked trees had laid on complete annual rings on the lower part of the bole after 1936 or 1937 (table 4). After laying on wood on only a portion of the lower trunk circumference for a year or two following these dates, all but one of these trees failed to lay on any wood at the base in 1939. This exception, tree No. 43, laid on wood only on the north quadrant. Thus, trees No. 50 and 47 had not laid on any wood at their bases for one and two years respectively prior to the ovipositions of 1939 and 1940 which constituted the beginning of successful attack on these trees. The majority of the additional unsuccessfully attacked trees, those with extensive etching of the wood, had not laid on any complete annual rings at their bases since 193 .

The failure of the trees to lay on wood a year or two prior to the beginning of successful attack was also noted frequently during the 1939 investigation and the previously mentioned study of girdled and partially girdled trees. This indicated conclusively that the trees were in a very weak and decadent condition before successful attack occurred.

Craighead (10), studying budworm defoliation of red spruce and balsam, reported the dropping out of annual rings at the base of the trees 1 to even 3 years preceding death. The stem analyses made during this investigation showed these to be true of hemlock dying from drought injury.

Table 4.--Year When Last Wood on Each Quadrant Was Laid on Trees in a Very Open Stand Produced by Old Blowdowns and Logging.

Tree No.	3	20	37	54	71	88
			Trees Successfully Attacked			
47	N-1938	N-1940	N-1940	N-1940	N-1940	N-1939
	E-1938	E-1939	E-1939	E-1940	E-1940	E-1939
	S-1938	S-1940	S-1940	S-1940	S-1940	S-1940
	W-1937	W-1939	W-1939	W-1939	W-1939	W-1938
48	N-1939	N-1940	N-1940	N-1940	N-1940	
	E-1937	E-1939	E-1940	E-1940	E-1940	
	S-1936	S-1938	S-1939	S-1940	S-1940	
	W-1936	W-1937	W-1937	W-1939	W-1940	
50	N-1938	N-1939	N-1940	N-1940	N-1940	N-1940
	E-1938	E-1939	E-1940	E-1940	E-1940	E-1940
	S-1938	S-1939	S-1940	S-1940	S-1940	S-1940
	W-1937	W-1937	W-1939	W-1940	W-1940	W-1939
			Trees Unsuccessfully Attacked			
56	N-1940 1/	N-1940 1/	N-1940	N-1940	---- 4/	
	E-1940 1/	E-1940 1/	E-1940	E-1940		
	S-1940 1/	S-1940	S-1940	S-1940		
	W-1940 1/	W-1940	W-1940	W-1940		
51	N-1939	N-1939	N-1940	N-1940	N-1940	N-1939
	E-1938	E-1939	E-1940	E-1940	E-1940	E-1939
	S-1938	S-1939	S-1939	S-1940	S-1940	S-1939
	W-1938	W-1939	W-1940	W-1940	W-1940	W-1939
45	N-1938	N-1940 3/	N-1940	N-1940	N-1940	N-1939
	E-1939	E-1940 1/	E-1940	E-1940	E-1940	E-1939
	S-1939	S-1940 3/	S-1940	S-1940	S-1940	S-1939
	W-1938	W-1940 1/	W-1940	W-1940	W-1940	W-1939
42	N-1939	N-1940	N-1940	N-1940	N-1940	
	E-1940	E-1940	E-1940	E-1940	E-1940	
	S-1940	S-1940	S-1940	S-1940	S-1940	
	W-1940	W-1940	W-1940	W-1940	W-1940	
52	N-1940 2/	N-1940	N-1940	N-1940	N-1940	---- 5/
	E-1940	E-1940	E-1940	E-1940	E-1940	
	S-1940	S-1940	S-1940	S-1940	S-1940	
	W-1940	W-1940	W-1940	W-1940	W-1940	
46	N-1939	N-1940	N-1940	N-1940	N-1940	N-1940
	E-1939	E-1940	E-1940	E-1940	E-1940	E-1940
	S-1939	S-1940	S-1940	S-1940	S-1939	S-1938
	W-1938	W-1940	W-1940	W-1940	W-1940	W-1940

54 All rings present on all disks.
Check Trees - All rings present on all disks.

1/ The 1938 ring was missing, and the 1939 and 1940 rings totaled less than 1/64 inch of radial increment.

2/ All rings since 1936 very narrow; 1937 and 1938 rings totaled less than 1/64 inch of radial increment.

3/ Very narrow rings in 1938, 1939, and 1940; these totaled only 1/64 inch of radial increment for the 3 years.

4/ Terminal 15 feet of tree a staghead caused by mechanical injury occurring about 1936.

5/ A dead 5-foot terminal with the last annual ring that of 1938.

Most of the successfully attacked trees and many of those attacked unsuccessfully had only partial rings or no 1940 summer wood on the terminal portion of their trunks. A comparison of the annual rings of the basal disks and the terminal disks from the trunks of the trees used in the root condition study showed that many of the trees had ceased laying on wood at their terminals 1 to 2 years after the last complete annual ring was laid on at their bases (table 4). Thus, when drought-killed trees die slowly, the last wood laid on is on that portion of the trunk in the lower half of the crown.

Stagheading alone, however, is not a reliable indicator of drought injury. Examinations showed that wind had sometimes caused stagheading by mechanical injury, such as partial breaking, whipping, or scarring of the upper trunk. When present, the latter injury was usually caused by a wind-thrown tree. When the stagheads were small the trees usually recovered, a lateral branch assuming dominance and replacing the dead terminal. In the case of stagheads resulting from drought injury, the stagheading was generally accompanied by a thinning of the foliage on the major portion of each crown and the trees did not usually recover. This was because stagheading in such cases was merely a stage in dying and complete shattering of the tree needles.

Twig and needle growth

Measurements of needle and twig lengths showed their annual growth trend to be another indicator of tree vigor.

Both needle and twig lengths were measured for 5 of the 1940 root study trees while twig lengths only were measured for certain other trees. The trees selected for needle measurements were 2 with successful borer attack (Nos. 47 and 50), 1 with medium unsuccessful attack (No. 52), 1 with

light unsuccessful attack (N . 54), and 1 with no borer attack (No. 55) The annual twig elongation fo 1938, '39 and '40 was measured to the nearest fiftiet of n i ch for 20 t rminal t gs from bra ches of the upper crown of ch ree. Simil r me ureme ts tak n of 20 branch terminals n the l we third o th c o of h t . Thi totaled 120 twig measurements per tree. Aft r t a e n al t ig elon tion was d termin d for e ch t ee, t three t ig ma surin ne est the v rage were selected and their n edles m as red to the near st fift h of n inch.

The growth t ends for t e t s n l s were p ctically the same. Th g th trends o th t i s and e l s of the u p r crown were found to be more r li ble indica o vi r t those o t lower crow , since the l tter w s more subject to c ta l al e vironmental influences such as shadin y neighbo i ; re . Th upper ro n of all the trees studied oc pi d m n n pos tion th ta d.

The vigo o s healt t ho e dec ded incr e in th ir 1939 twig growth over that of 1938. ro o th w s p are tly due to the change from the 1930 3 drou p d t t o favorable growing sea ons of 1938 nd 1939. T e d o re tt k. ree No. 54, with only v y light an cce f l bor tt show d subst ntial growth incre s i 1939 over that of 193 . Thi r o vio ly ld hav recovered from its drought i jury. Th , fail d to how any growth re ponse in 19 9 to the i p v t' s. Both their twig and needle le gths for t e 3 93. O ho g adu l d line in size Their 1940 twig along t o u lly 15 to 4 p rce t l . thar that of 1938. Ther was lso el , v l 1 ngth but this was not enough to be app ent l e. In one instance tree

No. 50, part of the br nches of the lower crown had not made any 1940 twig growth. These trees h d succ ssful b rer attack in 1940. The twig and needle growth of the unsucces ful borer- ttack d trees was intermediate between that of th succes ful borer-atta d trees and the borer-free trees. Those with he vy to m dium unsu c sful borer attack made about the same growth in 1939 in 1938 and how d a d cli e in their 1940 growth. Their failure to show improved growth in 1939 indicates their w aken d condition and probable d th in the near f ture.

RELATION OF G TH RESP E TO P CIPITATION

Revi w of Literature

The conflicting conclusions of ot er ers tt mpting to show the d pendence of gro t on pre i;itatio are outlined w ll by Burns (6). The findings of Bo (4), Stewart (37), r l (30), Lod ick (27), Diller (13), cIntyr and chnu 32), d Ly n (2 , 29) support the idea of a dependence of growth o pr cipit ti ile those of Hartig (20), Conard (8), Ha so and renk (1), d Sh (36) phasize oth r factors or the sum of ll fa tor . r t o t r st d in the earlier studie a good revi of the ork p blished pri r to 936 i iv n by Lyon (29).

Marshall, McIntyre nd Schnur, nd Lyo e studi of ea tern hemlock and found good correlations b tw p cipitatio and growth. In Massachusetts, Marshall made 10 y r summatio of growth and annual rainfall on 10 andy, well-dr in d sit . Oh p rly dr ined sites no correlation as found. In P s l nia McIntyr nd Schnur mad a statistical analy is of the c rrel tion twe n i l owth and precipitation for ll species of tre durin, the 20 ye i from 1914 to 1933. Comparing growth with precipitation f the p i of October to October,

January to January, and February to June, they state that no significant ratios were found, but the growth response did correlate more closely with precipitation for the 12 months of October to October than for any other group of months. They found that the 5 conifers, (hemlock, pitch pine, white pine, Virginia pine, and mountain pine), showed a distinct tendency to react more to the previous year's precipitation than to that of the year in which the increment was made. A correlation made between the growth of one year and the precipitation of the previous year (October to October) gave significant values for hemlock (4.0 to 4.3), pitch pine (2.8), and white pine (2.3 to 2.5). Ratios of 2.5 or over are considered significant. Although positive correlations were obtained in all cases the ratios for the other 8 species, in all but one instance, were too low to be significant. This was taken to indicate that a consistent growth lag was not evident for these species. Thus, although the correlation between precipitation and growth was not significant for all the tree species studied, it was significant for hemlock, which incidentally had the highest ratio of the 11 species. They found that white oak and certain other hardwood species have a higher ratio when growth is compared with the same year's precipitation, while conifers showed a distinct tendency to react more to the previous year's precipitation than to that of the year in which the increment was made. Certain hardwoods, such as red oak, occasionally showed a tendency to lag.

Bogue (4) had observed such a yearly lag. Instances of a lag are also mentioned by Lyon (28), Marshall (30), Stickel (38), and Diller (13). Diller, in discussing this lag effect, says that in each case it was found to be caused by an accumulated moisture deficiency from the drought of the preceding year or years. Because of the lag effect, it was practically

impos ible to correlate statistically the relation between rainf ll nd growth" even though the direct relat onship was appar nt. This state n by Dill r undoubtedly explains why 'cIntyre nd Sc nt (32) and Schumach r and Day (34) frequently found it i o si ic ly st tistical analys s to t significant correlations bet een g o' h of certain tree species and preci,- itation although in many case a direct rel tionship as apparent.

Lyon (29) mad a study of hemlock in Vermont and New Hampshire and concluded that the April throu,h Augu t p riod g ve the best correlation with the growth rate. He also found that the precipitation during the "snow-free p riod" (April through November) of the previous year, taken in conjunction with the April through August pr cipitation of the current y ar, provided an almost perfect accountirg fo the 32 critical years in the century (1835-1934) covered by his study. The April through November period of precipitation of the previous year accounted for the lag effect in the growth response for most of the years when th current year's growth response did not correlate directly with the April through August precipitation. Lyon (28) also studied certain hemlock growth da. taken by Douglass (14) in Vermont and found a correlation between this d ta and the precipitation.

Douglass (14) has poi ted out th t the ri gs of young trees tend to show a general lack of r sponse to single environmental factors. Later on the growth process does respond to ex er al factor ; hence the need to use the rings formed during th matur years.

Material and Method

This study is pr r i co ned w th the ro th and pr cipita tio d in th 1 0

ing and following it. The 15-year period, 1926 through 1940, was chosen. It is not the purpose of this report to attempt to judge which of the above methods is best. This literature has been reviewed merely to show where similarities and differences exist between the method used in this report and those used by Lyon, McIntyre and Schnur, et al. Ten permanent sample plots in areas that had not been logged or had not suffered noticeable blowdown injury were selected as good representatives of the stands in the hemlock type on the reservation. All were on gently moderately to well drained sites. Two trees of dominant crown class and mature age (near 200 years) were selected from each plot and 2 cores taken from them at breast height, one from the north quadrant and one from the south. This was considered sufficient since Lodwick (26) concluded that "the data from one radius on fifty seven trees are about as reliable as the data for four radii on the same trees." With the aid of a micro copp-caliper the cores were measured and the width of each annual ring determined to the nearest 0.01 mm. For the 20 trees the average annual radial increment for the period 1920 through 1940 was found to be 1.22 mm. The annual departure from this average for the period 1926 through 1940 is given in table 5 and figure 22.

Precipitation records at the Weather Bureau stations at Antigo and Wausau, Wisconsin 3/ were obtained from the time of their establishment in 1894 and 1895, respectively, through 1940. The towns are located, air-

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3/ Although there is a Weather Bureau station at Shawano, Wis., 22 miles south, airline, from the study area, the records could not be used because they were incomplete through the years used for the entire period.

T l , l r r .

Y	Average nt in d ha	Departure fr 21-y average 1/	Preci it t from th p A	Gro	N O	par re inch s 2/ H S	p il- ov	riod ber	3/	3/
1940	157	35	4.27	5.61	6?	5 4	6 56	4.7	6 3	2 5
1939	140	18	2 91	.44	0 73	1 3	3.13	11 5	12.2	12.4
1938	77	-45	5.57	8	15. 1	14.99	12.04	0.0	15 9	2 6
193	68	54	-2 81	-5 64	-6.18	.83	-5.97	-4.2	10.4	-9.3
1936	79	43	-1.32	1.36	1.7	. 69	3.64	-2.0	3 8	2 8
1935	120	-02	-1 2	-0 7	3 1	1. 4	1.47	2.5	0 7	4 5
1934	54	-68	64	1 31	-1 '6	3 9	5 17	-4.4	5.8	-8.1
19 3	1 6	-1	-0 0	- 71	3 ..	5	' 75	6	-10.8	2.3
1 32	70	-52	0	6		5.	9	9.	13 3	8 6
1	1 9	-03		.70		1			0 3	7 9
193	1		2.	1 2	5	3.27	.1	2		3.8
1		6	· 3	0 34	1	6	.54	6	7	8 2
9	1	1	- .96	4 9			7. 5	-1 3	.6	6 8
1	1	-0	0.64	.6	1	3 6	2.08	4 4	6 5	6 7
19 6	10		1 6	3. 9			1	4 5	0 6	1
1925			3	84		4 3	.75			

1/ Th p u i o e
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3/

[illegible] st, [illegible]ly th[illegible] study [illegible] Th[illegible] [illegible] on [illegible] these stations was deter[illegible]ne for the sp[illegible]g [illegible]as n (Ap[illegible] [illegible] Jun[illegible], the growing season (April thro[illegible] August), th[illegible] an w-fl[illegible] [illegible]e ior [illegible]u [illegible] thr[illegible]gh November), th[illegible] Octobe[illegible] th[illegible]ough Septe be[illegible] n u[illegible], a[illegible]d the cale[illegible] r year. The mean of each of the five p[illegible]riods wa[illegible] determi[illegible]ed fro[illegible] th[illegible] ti[illegible]e o[illegible] each station's establishment throug[illegible] 1940 a[illegible]d these w[illegible] re averag[illegible]d to [illegible]ve [illegible]n "average mean for the two stations Figure 21 given t[illegible] ir av[illegible] [illegible] m[illegible]l and growing season departures during t[illegible]e last three dec[illegible]des. This show[illegible] the extreme dry summers of the 1930-37 period and the high annu[illegible]l [illegible]prec[illegible]pi[illegible]tio[illegible] of the 3 years preceding the drought. [illegible]ince this stud[illegible] is prim[illegible]rily concerned with the 1930-37 drought period th[illegible] [illegible]preci[illegible]itatio[illegible]d partur[illegible]s of t[illegible]ble 5 are confined to the years 1925 to 1940.

Seve[illegible]al methods of correlati[illegible]g precipitation with tree growth were tried[illegible] In atte[illegible]pting to fi[illegible]d a preci[illegible]pitation period that would give a perfect direct corr[illegible]latio[illegible] [illegible]ith g[illegible] th, 7 different periods and more than 10 combinations were u[illegible]ed. [illegible] [illegible]n of the precipitation periods were compared with g[illegible]owth on the ba[illegible]is of growth made during the same year that precipitation oc[illegible]urred, and that made the follo[illegible]ing [illegible]ear. These included the October to Octob[illegible]r p[illegible]riod u[illegible]d by [illegible]cIntyre and Schnur and the April through August period used by Lyon. Th[illegible] conclusions reached by these authors and the results obta[illegible]ned when [illegible]he[illegible] me[illegible]hods [illegible]e applied to the data of this [illegible]udy indica[illegible]ed that a [illegible]ean pr[illegible] c[illegible]'p[illegible]t[illegible]ation value based on the precipitation of both the current and pr[illegible]ceding yea[illegible]s might give a better correla[illegible]t'on with gr[illegible]h than that obt[illegible]o when only one season's precipitation con[illegible] r[illegible].

No[illegible] [illegible]o w[illegible]ct[illegible]l[illegible]y [illegible] [illegible]rfect direct correla[illegible]io[illegible]r

ry a r, f t l t or el tions as obtained by c bini g t p c it ta d tu from the average of the preceding y r's grow i g o it t e d parture from the av rage of the current y ar s ri s n (colu A, t le 5) nd compari g this valu ith t c nt t . F c rt in ye r , n ev n closer c rrela- ti s e t tob through S pt ber d parture for the e t d h l in c lu A. Th um of the e is i n i o 3 t d as the adva tage of t king into consid r tio t e t of oth th precedi and current aso th r ti ng l g o th riod, nd giving d ble w ig to the p c l of t e r nt spring sea n. Figure 22 sh t l r , t recipit tion val s of columns A and B h n th d p tu es are expr ssed in hund dth milli meters of owt and ch s o p i,it tion.

The v lues in colu n , ta le 5, were obtained by combining the departure of the current ye 's gro.in season with that of the snow-free period (April through Nove.ber) of the preceding year. This combination was suggest d t the uthor by th conclusions reached by Lyon (29). In his paper Lyon did not combine the values for these 2 periods but merely us d one in co junction ith the othe . Figure 22 shows the relationship betwe en the lues o column C nd hemlock growth. All thr e hoices of precipitation per ds giv in igure 22 show a ge eral di ect relation- s ip between precipi ation and g o th. For these data, at least, the B column values give a slightly better direct correlation than the others, although the C values are a clo e second. For the 15-year period (1926-40), the precipit tion valu s of column B show a direct relationship between the

precipitation and annual radial increment trends for all but 4 years. A direct trend relationship was not shown in 1930, 1939, and 1940 due to a lag in tree growth response to changes in the precipitation trend. The remaining exception, 1934, is also due probably to a lag effect and is discussed later.

The 1938 growth, figure 22, shows that following several years of well below normal precipitation there is a definite lag in the growth response to a period of above normal precipitation. A similar lag is shown in 1930 when the change in the precipitation trend was in the opposite direction. In both cases there is a lag of one year. Similar instances of a lag in growth have been mentioned by Diller (13), Lyon (29), and others. They have been discussed previously in the review of the literature.

Figure 22 shows irregularities between the growth and precipitation trends in 1928, 1933, and 1934. Reference to table 5 will show that above normal annual precipitation in 1927 together with very heavy precipitation during the latter half of the 1928 growing season was sufficient to counteract any effect the dry spring of 1928 might have had on the 1928 growth. In 1933 practically normal precipitation during the spring season was apparently responsible in a large measure for the upswing in growth that year. The 1934 low in tree growth was undoubtedly the result of the gradual lowering of the water table due to the accumulation of consistent annual deficiencies from 1930 to 1933 inclusive. It undoubtedly would have been evident in the 1933 growth also had not the practically normal precipitation during the spring season that year replenished temporarily a portion of the depleted soil moisture supply of the upper layers of the

soil. The 1935 growth response shows the effect of above average precipitation during the 12-month period (October through September) much of which occurred in the fall of 1934 (principally November) prior to the freezing of the ground. Thus, above normal precipitation in the fall of 1934 followed by nearly normal precipitation during the 1935 growing season resulted in an upswing in the growth trend.

Conclusion

The author believes that figure 22 shows a good correlation between precipitation and growth. In the hemlock borer study a summation precipitation value based on the precipitation departures from the average for both the current and preceding years gave a better correlation with growth than that obtained when only one season's precipitation was considered. The author considers the 15-year period entirely too short to determine which is the best of the numerous possible periods of precipitation that may be chosen for correlating with growth. However, it is believed that a method using a summation or mean precipitation value based on the precipitation of both the current and preceding years will give a better correlation when correlated with the current year's growth than a method based on either season's precipitation taken separately. This phase of the study suggests a new approach to the problem of correlating growth and precipitation.

The studies on root condition and annual ring growth have shown that hemlock is very sensitive to precipitation changes. This agrees with the statement made by McIntyre and Schnur (32), "It is significant that extreme losses of hemlock occurred and that the increment data indicate

that this species is highly sensitive to precipitation." Stickel (33), studying drought injury in hemlock-hardwood stands in southern Connecticut, observed that ". . . the deficient precipitation of the last five years appears to have its greatest effect on hemlock."

NATURAL FACTORS LIMITING BORER ABUNDANCE

Factors having a direct effect

An attempt to determine the natural mortality of the hemlock borer during the egg stage was only partially successful. During the 1938 and 1939 oviposition studies the location of more than a hundred eggs was marked in the field, and blocks of bark containing other eggs were brought into the laboratory for observation. Examination of the eggs without disturbing or injuring them was difficult. Many of them were ruined when the crevice in which they were attached was spread slightly to permit examination. In the field, ants removed many of the eggs. Satisfactory data were obtained on only a small percentage of the eggs. These indicated a high egg mortality. Parasites and predators, together with other environmental factors, caused a mortality in excess of 70 percent on certain trees.

Normally there is relatively little winter mortality. Bi-monthly examinations were made during the winter of 1938-1939 and two examinations were made during the winter of 1939-1940. These indicated that in material affording the larvae a favorable habitat the mortality is very low, never exceeding 10 percent. Therefore, winter mortality is of relatively little importance as an environmental control of the hemlock borer.

Parasites.--During the course of the investigation 6 parasites of the hemlock borer were found. These were, in order of their importance,

Atanycolus n. sp., Odontaulacus bilobatus (Prov.), Spathius n. sp. Coeloides n. sp., Deuteroxorides borealis (Cress.), and Ichneumon n. sp. Four of these are shown in figure 23. A seventh species, Odontomerus canadensis (Prov.), was obtained from caged material that was heavily infested with hemlock borers. This species may also be a parasite of the borer although it was not actually observed feeding on larvae as were the other species. One egg parasite, a pupa of a Telenomiid, was found but it was not possible to identify it to species in this stage of development.

Quantitative data were collected during two seasons to determine the effectiveness of parasites as a control factor. A survey was made each fall by following the logging crews on salvage operations. To obtain a more representative selection bark samples were taken from each tree at 16-foot intervals along the trunk. These samples were about 1 foot square, and the borer population was determined by counting the number of emergence holes and adding the number of mature larvae in the bark. The parasite population was determined by counting the number of cocoons. Usually 10 to 20 trees were examined in each area. These gave a population count large enough for an adequate sample. For example, on 115.6 square feet of bark chipped from 16 trees with mature borer populations, 584 beetles and mature larvae had survived while 720 had been killed by parasites.

Only two of the previously mentioned species were found to be present in sufficient numbers to have an appreciable effect on the hemlock borer population. The average parasitization by these, Atanycolus sp. and Odontaulacus bilobatus, in the areas examined was 40 to 50 percent. High parasitization was found on individual trees, but for the trees of any area the highest was 55.2 percent. The aggregate parasitization by the other

species was less than 1 percent. It is doubtful if parasites will ever prove a satisfactory control agent for the hemlock borer.

Since published information concerning the life history and habits of these parasites in this region was not available, a limited amount of biological data was collected. The flight of Atanycolus sp. began about the middle of May and continued into September. The peak of emergence occurred during the first half of June. Due to some emergence in both July and August it is evident that this species has a long flight period. In the field, it was rarely observed after the first of September although under cage conditions some adults lived until September 12. During July a period of approximately 30 days elapsed from the time the mature larvae spun cocoons until they emerged as adults. The adult of this species of Atanycolus (fig. 23,A) is from 6 to 10 mm. long. The head, thorax, legs, antennae, and wings are black and the entire abdomen is bright red. During the period 1938-1940 there was a noticeable increase in the population of this parasite on the Menominee Indian Reservation. During 1938 O. bilobatus was more numerous than Atanycolus, but this was reversed in 1939 and 1940.

The cocoons of Atanycolus sp. (fig. 24,C) can be readily distinguished from those of O. bilobatus by their pill-box shape. They are from 7 to 11 mm. long and 3 to 4 mm. wide, of a tan color, oval in shape, and flattened dorso-ventrally so as to give them the appearance of a pill box. The males are usually smaller than the females and their cocoons are correspondingly smaller. In this study the cocoons were always found in the galleries between the wood and the inner bark.

The flight of O. bilobatus began about the middle of June. The peak of emergence occurred about July 1 and the flight continued into the

first half of August. Mature field-collected larvae, placed on cotton batting and caged individually in glass vials, completed their pupal period in 20 days under laboratory conditions. The adult (fig. 23,B) has an all black body except for a red band around the mid-portion of the abdomen, the legs and antennae are black, and the wings are clear and transparent. Two instances were found in which the red band was absent and the abdomen all black. This, however, is very rare. The body length is usually 8 to 12 mm. The cocoon is oval-shaped, about 14 mm. long by 4 mm. wide, very thin-walled, semi-transparent, and of a light tan tint. It is usually located in the inner bark. Since the cocoon (fig. 24,A) adheres to the bark of the gallery walls, it is nearly always torn in removing the bark.

The flight of Spathius sp. began early in June. Two distinct periods of emergence occurred, one during the second week of June and the other in September. This indicated either two generations or two different broods each season. Under cage conditions, the adults of this species usually lived two weeks, but some individuals lived 16 days or longer. This parasite is gregarious, from 4 to 8 larvae maturing on one hemlock borer. The cocoons are spun adjacent to one another (fig. 23,D) and all the adults emerge through the bark by the same exit gallery. The adult (fig. 23,C) is a small wasp-shaped insect, about 4 mm. long, with a solid brown-colored body. The wings are clear and transparent except for several brown-pigmented areas. These irregular areas give the wings a general mottled appearance.

The flight period of Coeloides sp. was not determined but specimens were collected in the field during June and July. The color pattern of this species is similar to that of Atanycolus sp. but the individuals are generally smaller in size and the scape or basal segment of the antennae is not pedicellate as in Atanycolus.

The other species were not found in sufficient numbers to obtain any detailed information regarding their periods of flight.

Predators.--Woodpeckers destroy many of the mature larvae, particularly during the winter months. They chip off the outer bark in order to reach the larvae. This exposes the inner bark and makes the trees very noticeable because of the bright red color. Occasionally, nearly all of the outer bark is removed from the bole of a heavily infested tree. At least five species were observed. These were the red-headed, downy, hairy, and pileated woodpeckers and the yellow-shafted flicker. Although their work is more spectacular, it is usually so spotty that as a factor of control woodpeckers are generally not as effective as parasites.

Ants removed many of the eggs from certain of the trees on which incubation period data were being taken. On many trees 15 to 40 percent of the eggs were removed. Although most of this was done by ants, a small amount was done by other insects.

Factors having an indirect effect

Climatological factors.--Climatological phenomena, such as drought, high temperature, and high winds, were observed to have primary influence on the hemlock borer situation on the Menominee Reservation. The effect of drought has previously been discussed and data presented to show the relationship between hemlock growth response and precipitation. Extreme heat has characterized the majority of the growing seasons of the 1931-37 period. For example, on July 11, 1936, the temperature at Neopit reached 110° F. in the shade. This unusually severe heat wave was broken by a tornado-like wind that blew down 30,000,000 board feet of timber in the Menominee Reservation alone. According to Heritage (21) there was particularly

serious blow-down damage in 1933, 1934, and 1936 which resulted in the loss of 80,000,000 board feet of timber. In addition to the timber loss caused by the mechanical effect of these winds, there was undoubtedly considerable loss due to the sudden subjection of the under-story trees to full sunlight, heat, and high evaporation at a time when there was a deficiency of soil moisture. Baker (1) states that under these conditions such trees suffer considerable injury or die. The hemlock trees particularly suffered injury from heat and exposure. A study of tree mortality between 1937 and 1940 showed the hemlock mortality in the blow-down injured areas to be nearly double that of the areas not injured by blow-down.

To determine the relationship of climatological and site factors to hemlock mortality and borer abundance, 55 permanent ½-acre sample plots were established on the Menominee Indian Reservation in 1937 and 1938 by the Bureau of Entomology and Plant Quarantine. The majority of the 49 plots established in 1937 were in mature stands of pure or nearly pure hemlock. The six plots established in 1938 were in thrifty, mixed hardwood-hemlock stands. The 55 plots were all examined annually in 1938, 1939, and 1940 for tree mortality and borer infestation. In 1940 diameter measurements were taken for all trees to determine the amount of growth made since the establishment of the plots. Many of these plots were in areas that had been logged just prior to the establishment of the plots while others were logged during the period of this investigation. Others were in severe blow-down injured areas and in non-injured virgin stands. Thus, many variations of stand density were represented. Diameter measurements and detailed data regarding time of breakage or cutting were taken for all stumps on each plot in order to determine the former as well as the present

stand density. To determine the growth trend of each plot, two increment cores were taken from six selected trees - three dominant and three co-dominant. The average diameter at breast height was obtained for the trees in the dominant and codomirant classes of each plot and cores were removed from the north and south sides of the three trees nearest this average. The annual increment was measured to the nearest hundredth of a millimeter in a special increment corer measurer. A portion of the increment core data has been presented and discussed previously in the section concerning the relationship between growth and precipitation.

In 1938, similar data were taken for eight quarter-acre permanent growth study plots established in 1929 by the forestry department of the Menominee Indian Reservation.

Forty-four of the 1/2-acre plots were selected to study the effect of exposure and site change on hemlock mortality following a sudden opening of the stand. All the plots were in stands of the hemlock type. Twelve were in areas that had suffered severe blow-down injury during the wind storms of 1933-36. Salvage logging operations conducted in these areas following the wind storms removed all the merchantable blow-down and drought-killed trees present at that time. This is the reason that when the plots were established in the fall of 1937, the accumulated volume of dead timber on these plots was usually less than that found on the 32 plots in stands not injured by blow-down. Many of the latter were in virgin stands where neither logging nor salvage operations had been made and the balance were in stands where only light salvage cuts were made to remove the more accessible drought-killed trees.

During 1938-40, the hemlock mortality on the 12 plots injured by the 1933-36 wind storms was double that of the 32 plots in stands not so in-

jured. The average annual hemlock mortality percents, by volume, for these 12 plots during this 3-year period was 25.3, 11.8 and 1.0 as compared with 10.2, 4.9 and 0.5 for the plots in the non-injured stands, table 6.

The volumes given in table 6 include only trees of 9 inch d.b.h. and over. Determined from the 1937 d.b.h. measurements, the average gross volume of green timber on these plots in the fall of 1937 was, in round numbers, 13,000 board feet per acre for the plots of the blow-down areas and 20,000 for the check areas. The approximate average volume of living trees per acre for each year thereafter, columns 3 and 7 of the table, was determined by subtracting the annual mortality volume for that year from the green tree volume of the previous year. Since these plots were all in nearly pure hemlock stands, the annual mortality for all species other than hemlock was very small and is not given in table 6.

Table 6.--Annual Hemlock Mortality in Blow-down Injured and Non-injured Stands (Gross Volume - B.M.)

	Stands Injured by Blow-down				Non-injured Stands			
Year	Number of Plots	Approximate Ave. Annual Volume of Green Trees per Acre	Average Dead Hemlock Volume per Acre	Hemlock Mortality Percent	Number of Plots	Approximate Ave. Annual Volume of Green Trees per Acre	Average Dead Hemlock Volume per Acre	Hemlock Mortality Percent
1937	12	13,000	1,828	--- 1/	32	20,000	3,602	--- 1/
1938	12	10,000	3,291	25.3	32	18,000	2,033	10.2
1939	12	9,000	1,183	11.8	32	17,000	885	4.9
1940	12	9,000	92	1.0	30	17,000	87	0.5

1/ The dead volume given for 1937 does not indicate the annual mortality for that year, but merely the volume of dead trees present when these plots were established in the fall of 1937.

Yellow birch ranked second to hemlock in mortality volume. The heaviest mortality for this species during 1938-40 was in 1938 when an average of 101 board feet per acre occurred on the group of 32 plots previously mentioned. The total mortality volume that year for all other tree species present on these plots was 189 board feet per acre. Thus, on plots where the 1938 hemlock mortality was 10.2 percent, the yellow birch mortality was 0.5 percent and the total mortality for the balance of the tree species present was 0.9 percent.

The volume data for the permanent sample plots agree remarkably well with data collected by Forest Supervisor Delaney and the Indian Service in a strip survey made on the Menominee Indian Reservation in November 1938. The gross volume in board feet per acre of green timber for the hemlock type was about 11,000 for the logged areas and 18,000 for the uncut areas. This survey considered only trees of 10-inch d.b.h. and over. As shown in table 6, the 1938 green tree volume on the sample plots was about 10,000 board feet per acre for the blow-down injured stands and 18,000 for virgin stands and stands having only a light salvage cut.

The author believes that the difference in the hemlock mortality of the plots in the old blow-down areas and their check plots is largely the result of heat and exposure injury following the opening of these stands by blow-down. Much of the mortality that occurred the first year following blow-down injury might be chargeable to mechanical injury inflicted during the storm. The blow-down plots selected for this analysis were in areas that had suffered their major injury in either 1933 or 1934 and had little or no injury from the 1936 storm. Thus, ample time had elapsed for any mechanical injury effect to have made itself evident. The con-

sistent relationship shown in table 6 between the annual mortality trend for the two groups of plots further indicates that the difference was not due to any carry-over effect such as mechanical injury. This consistent relationship indicates that the factor responsible for this annual mortality difference is still operating on the blow-down plots and causing a consistently greater mortality than it is on the check plots. A carry-over effect on the other hand gives a changing rather than a consistent trend. For example, the general downward trend of the 1938-40 hemlock mortality for both groups of plots is due to the carry-over effect of the 1931-37 drought period. This indicates that during the 1938-40 period heat and exposure were largely responsible for a doubling of the hemlock mortality rate on the reservation in open stands of the hemlock type that had a stand density of only about 10,000 board feet to the acre or less.

Table 6 indicates the tree mortality trend of the 1938-40 period. In order to explain more fully the causes that produced the heavy hemlock borer population of 1936-39, the stump tally taken for each of these plots was used to determine their approximate stand volume in 1930 and their hemlock mortality volume for the period 1931-37. This indicated that many of the plots, on both the blow-down areas and the check areas, had been in stands having a volume of 20,000 up to 32,000 board feet to the acre. The hemlock mortality during the decade following 1930 had reduced the average volume of green timber on the hemlock type areas severely injured by blow-downs by about 60 percent. Occasional areas were seen and one sample plot was located in an area where the mortality was nearly 100 percent. In areas where there was no appreciable blow-down injury, and virgin stands or very light selectively logged stands predominated, the hemlock mortality

for the same decade was usually 15 to 20 percent. For all the reservation sample plots, the hemlock mortality during 1931-40 was about 25 percent. The greater part of this mortality occurred within the 5-year period, 1934-38. This percentage appears to be about right for the reservation also, since it is approximately the same as that of the 1938 Indian Service survey which showed a hemlock mortality volume of 135 million board feet during the last 5 years and an inventory of about 400 million board feet of living hemlock.

The sample plot studies clearly showed that unfavorable climatological conditions during 1931-37 were the principal factors responsible for the heavy hemlock mortality of 25 percent, by volume, that occurred on the Menominee Indian Reservation during the decade 1931-40 and resulted in the building up of an epidemic hemlock borer population in 1936-39. The principal climatic conditions responsible for the mortality were drought, heat, and wind. In 1940 a noticeable decrease in the borer population was apparent for the first time. This indicated that the population trend was on the decline, and as would be expected of a secondary insect, it was following the tree mortality trend.

Site factors.--Through their effect on the host trees, the site factors indirectly affect borer abundance. As the condition of the host trees was found to be the principal factor regulating borer abundance, the climatic and site factors as a whole have a more primary influence on the borer population than do the parasites, predators, and certain other factors that affect the population more directly. The more favorable the site conditions are for the maintenance of a healthy, vigorous hemlock stand, the less favorable are the conditions for the larval population. The site factors studied were soil type, soil fertility and stand density.

Much of the hemlock in this region is found on a marginal or border type site. The soil of such a site is too low in fertility to support a hardwood stand, but hemlock can successfully maintain itself as long as other environmental factors are favorable. Most of it is nearly pure sand, usually over gravel, and it has a low water holding capacity. It becomes a poor site even for hemlock as soon as one of the principal environmental factors, such as precipitation, ceases to be favorable for any lengthy period.

Since the soil type determines the water holding capacity of the soil, during the drought it became a primary factor in determining the tree mortality and the borer population. In the sample plot studies, it was found that during the 1931-40 decade the hemlock mortality in hardwood-hemlock type stands was generally less than in hemlock type stands. This appeared to be due primarily to three factors. First, because of their deeper root systems the hardwoods were less susceptible to drought mortality. Thus, tree mortality caused fewer holes in the stand canopy so that heat and exposure did not have as much effect on these stands as on the hemlock type stands. Second, the hardwoods in general demand a better soil type. Thus, the hardwood-hemlock stands were nearly always on a sandy loam soil while the hemlock type stands were usually on a nearly pure sand soil that had a lower water holding capacity and less fertility than a sandy loam soil. Third, the hardwood leaves produced a thicker leaf litter than the hemlock needles, and the hardwood-hemlock type stands had a thicker layer of leaf litter to protect their surface soil from heat and moisture evaporation.

Man has little or no control over the previously discussed climatic and site factors. However, by proper cutting practices and timber management he can regulate stand density to a certain extent. When closed

stands are suddenly opened by heavy logging, drought, blow-down or other causes the residual hemlocks frequently suffer windthrow and heat injury. The exposure of the soil for long periods to direct sunlight causes high soil temperatures, dries out the duff layer, and has a detrimental effect on the small tree roots in the surface layer of soil. The following plots are discussed in detail because they show the tree mortality during the entire drought period in areas ranging in stand density from one in which 50 percent of its volume was removed by logging prior to the drought period to another in a virgin stand having an average of 35,000 board feet to the acre. They also show the mortality in both hemlock type and hardwood type stands.

The 8 quarter-acre growth study plots established in 1929 by the forestry department of the Menominee Indian Mills were the only permanent sample plots on the reservation prior to the 1930-37 drought. These were examined in 1935 by the forestry department, and in 1938 by the writer in cooperation with this department. The total mortality of hemlock during the 9-year period 1929-38 in the plots where this species predominated (Nos. 3, 4, 6, 7, and 8) was 61 trees, or 32 percent. Only 2 of the 33 hardwood trees of these 5 plots were killed during this 9-year period, 1 by knock-down and 1 by blow-down. Death of only 2 of the 61 dead hemlocks could be attributed directly to blow-down. The 1929-38 tree mortality for each plot is given in table 7.

Three plots (Nos. 6, 7, and 8), located in the same general area, showed decided differences in their hemlock mortality. Plot 6 is located on a small levee-like ridge with rather steep sloping sides and is well drained on all sides. The stand was heavily cut over during a logging operation just prior to 1929, about 43 percent of the volume being removed.

Table 7

1929-38 Tree Growth Rate
Menominee Indian Reservation
Forestry Department Permanent Sample Plots

Plot No.	Total Trees Fall 1929	Hemlock Fall 1929	Green Trees at Close of 9-yr. Period	6-yr. Period 1929-35 Inclusive; Total D.B.H. Increment Inches	6-yr. Period 1929-35 Inclusive; Ave. Annual Diam. Incr. Inches	6-yr. Period 1929-35 Inclusive; Trees Dying in Period	6-yr. Period 1929-35 Inclusive; Trees Wind-broken	3-yr. Period 1936-38 Inclusive; Total D.B.H. Increment Inches	3-yr. Period 1936-38 Inclusive; Ave. Annual Diam. Incr. Inches	3-yr. Period 1936-38 Inclusive; Trees Dying in Period	3-yr. Period 1936-38 Inclusive; Trees Wind-broken	1929-38 Tree Mortality by Species (Percentage) Hemlock	1929-38 Tree Mortality by Species (Percentage) Hardwood
1	32	2	Hemlock 1	1.7	.028	1	0	.5	.017	0	0	0	
			Hardwood 24	13.0	.093	2	0	9.2	.127	1	0		10
2	40	5	Hemlock 5	1.4	.047	0	0	1.0	.066	0	0	0	
			Hardwood 33	17.9	.090	1	0	6.8	.068	1	0		6
3	45	38	Hemlock 31	12.2	.066	7	0	8.4	.090	0	0	19	
			Hardwood 7	3.0	.083	2	0	2.6	.144	0	0		0
4	36	31	Hemlock 27	17.6	.109	2	0	10.8	.133	2	0	13	
			Hardwood [2] 5	1.9	.063	0	0	1.5	.100	0	0		0
5	21	2	Hemlock 2	0.9	.075	0	0	0.5	.083	0	0	0	
			Hardwood 17	13.8	.135	1	0	7.8	.149	0	1		9
6	69	66	Hemlock [1] 33	9.9	.050	17	0	5.6	.056	14	0	47	
			Hardwood [2] 3	1.2	.068	0	0	0.5	.055	0	0		0
7	36	34	Hemlock 17	5.8	.057	5	0	4.2	.041	11	1	50	
			Hardwood [2] 2	.2	.016	0	0	.1	.017	0	0		0
8	39	23	Hemlock 21	5.7	.045	0	1	3.1	.049	1	0	9	
			Hardwood 16	4.8	.050	0	0	4.7	.098	0	0		0

[1] Two green trees omitted from growth calculation due to contradictory diameter measurement records. These are included in the mortality calculation.

[2] All birch trees, majority of which were suppressed trees.

A tally of the stumps in 1938 showed a total of 41 within the borders of the plot. Of this number, 23 hemlocks of 10" d.b.h. or over, having an estimated volume of 3,400 board feet, had been cut in the previously mentioned operation. Three white pines with an estimated scale of 1,860 board feet had been logged about 40 years earlier. If the volume of these pines were included, the percent by volume removed by logging from this plot would exceed 50 percent. Sixty-nine trees, nearly all hemlocks, with a total volume of about 4,450 board feet, remained after logging, and all were living when the sample plot was established in 1929.

During the period 1929-38, 31 of the 66 hemlocks on this plot died (17 prior to the fall of 1935 and 14 more prior to the fall of 1938). These trees represented a merchantable volume (trees over 9" d.b.h.) of about 1,350 board feet, or nearly one-third of the residual volume left by the logging operation (table 8).

Plot 7 is located in a practically pure hemlock stand. The plot is on the top of a low, flat ridge and is well-drained. The area was selectively logged in 1930, and 10 trees on the plot were cut. These trees represented a volume of approximately 1,200 board feet, or about a 17 percent cut.

During the 1929-38 period, 16 of the 30 hemlock trees of this plot died, 5 prior to the fall of 1935, and the remainder between then and the fall of 1938. Six of these trees were in the 20" to 28" d.b.h. group and 4 in the 16" to 18" group. Because the majority of the dying trees were from the large diameter classes, these trees totaled 3,890 board feet, or about two-thirds of the volume of the stand.

Plot 8 is just outside the area cut selectively in 1930. The plot contains a mixed stand of hemlock and hardwoods and has not been logged.

Table 8

Gross Volume Table - in Board Feet
Menominee Indian Reservation
Forestry Department Permanent Sample Plots

Plot No.	Green Timber: Maple	Green Timber: Other Hardwoods	Green Timber: Hemlock	Green Timber: Total	Dead Timber: Hardwoods	Dead Timber: Hemlock	Dead Timber: Total	1938 Volume Green & Dead	Volume Removed Based on Stump Diameter: Hardwoods	Volume Removed Based on Stump Diameter: Hemlock	Volume Removed Based on Stump Diameter: Total	Approximate Volume in Recent Past (Prior to 1929) 3/: Per Plot	Approximate Volume in Recent Past (Prior to 1929) 3/: Per Acre
1	1,636	290	70	1,996	0	360	360	2,356	1,580	0	1,580	3,936	15,700
2	611	2,420	0	3,031	20	0	20	3,051	950	120	1,070	4,121	16,500
5	1,253	1,040	0	2,293	250	0	250	2,543	3,040	140	3,180	5,723	22,900
6	All Hardwoods	400	2,700	3,100	0	1,350	1,350	4,450	1,860 1/	3,400	5,260	7,850	31,400
7		160	1,670	1,830	0	3,890	3,890	5,720	600	600	1,200 2/	6,920	27,680
8		5,070	3,410	8,480	0	270	270	8,750	0	0	0	8,750	35,000

1/ Total volume for three white pine trees. No hardwood of merchantable size cut on this plot. These pines had been cut long before 1929 (probably 40 years previous). Therefore they are not included in calculation of "volume in recent past".

2/ Estimated volume. Complete stump diameter records not available for this plot. Ten trees, seven of merchantable size, had been cut. Aggregate volume for six of these trees was 940 board feet. Estimated volume for other four trees conservatively placed at 260 board feet.

3/ Data on the volume increment due to growth during this period of 20 years or more are not available. This calculated volume therefore exceeds the actual volume present by the amount of the volume increment.

It is located about one-half mile west of plot 7, on the top of the same ridge. The site conditions for this plot are slightly better than for the other two, although the soil differences between plots 8 and 7 are much less than those between plots 8 and 6.

During the period 1929-38, only two hemlock trees in this plot died. One, a 12-inch (d.b.h.) tree, died prior to the fall of 1935 when its top was broken off at 35 feet, probably by wind. The second tree died apparently from natural causes. This tree was of intermediate crown class, 15" d.b.h., had been dead for about two years, and had the shoestring rot (Armillaria mellea) on all the main roots and evidence of very light hemlock borer attack. The latter was entirely too light to have had any part in causing its death. A "ring count" showed a 17-inch (d.b.h.) codominant hemlock to be 240 years old. The majority of the larger trees of both this plot and plot 7 are from 250 to 275 years old.

A comparison of these three plots brings out the strikingly low tree mortality of plot 8, which was only 9 percent as compared to 47 percent and 50 percent mortality for plots 6 and 7, respectively. It is the opinion of the writer that drought and heat, causing high soil temperatures, were responsible for the high tree mortality of plots 6 and 7. The logging operations preceding the hot, dry seasons intensified the injury in proportion to the amount of opening and exposure caused by the operation. In the case of plot 7 the overmaturity of many of the dominant trees made them less resistant to the drought. This stand had also been opened to a limited extent by logging, although to a less degree than had plot 6. As the trees became more weakened and the death of some of them opened the canopy, the mortality rate increased fourfold during the last 3 years (1936-38). Plot 6 clearly illustrates that in a hemlock type stand a

logging operation should not remove 40 or 50 percent of the stand volume in a single operation even in a dense stand of over 30,000 board feet to the acre. Both plots 6 and 7 will be referred to later in this report in the portion on control and cutting practices.

On plot 8, 16 hardwood trees composed 58 percent of the volume. Two-thirds of these hardwoods were between 16" and 28" d.b.h. and their crowns formed quite a protective canopy over the area. Although many of the hemlocks in this plot were as old as those of plot 7, the protection from exposure and heat afforded them by the hardwoods more than offset any limited effect which age might have exerted. This example illustrated the primary nature of drought and heat as compared to overmaturity and other subordinate factors which have had a minor part in bringing about the present decadent stand condition.

The generally greater diameter growth and lower tree mortality on the hardwood plots, table 7 (1, 2, and 5), indicate that the hardwood stands as a whole suffered less severe injury from the drought than did the hemlock. This is principally due to the fact that the hardwoods in general have a deeper root system and demand better site conditions. This agrees with and substantiates the explanation offered earlier for the lower tree mortality of the hemlock-hardwood type than of the hemlock type.

Plots 3 and 4 are near a creek that remained constant through practically all of the drought period. One plot is 1 chain and the other about 4 chains removed from the creek. This stream tended to maintain a more constant water table in this vicinity and explains the low hemlock mortality on these plots. Because of the tendency of the stream to minimize the drought effect on these plots, the volumes for these plots are not

considered in table 8.

CONTROL

Since the hemlock borer has been shown to be definitely a secondary insect, direct control methods are not necessary or economically justified by their insect control value. However, during the course of this study certain information was obtained that has a bearing on control and is also economically sound because it also constitutes good forestry practice in handling mature hemlock type stands.

A criterion developed for identifying dying hemlock trees

The salvaging of recently dead and dying hemlock tends to have a control effect on the borer population to the extent that such operations reduce the volume of favorable brood trees available on the forest.

As discussed earlier in this report, hemlock does not usually shatter its needles until 2 or 3 years after it is definitely in a dying condition. In 1938 the forestry department of the reservation expressed an urgent need for a method of detecting these dying trees in order to increase the efficiency of their salvage operations. Another economic factor during the late drought years when the hemlock mortality was high was the fact that since market conditions and their mill capacity would not permit the handling of more than 15 to 20 million board feet of hemlock salvage annually, the local pulp mills became the chief purchasers of the surplus hemlock salvage logs. They could not use logs that had more than 1½ inch of sap rot. Thus, trees that had been dead more than 3 years could not be marketed.

During 1938 and 1939 a criterion, based on certain crown and stem

characters, was developed for detecting dying hemlock trees 2 years prior to complete loss of foliage. These characteristics, which are discussed in detail on pages 17 and 18, have been repeatedly tested and found to be satisfactory. With their aid, it was now possible to mark more efficiently and increase the period between salvage operations by at least 2 years.

Winter decking of infested logs

The study of the effect of temperature on the rate of development of the borer populations of decked logs has shown that the peak of beetle emergence from logs decked in the shade was 2 to 4 weeks later than that of similar logs decked in the open. This would indicate that when it is necessary to leave infested logs in the woods until after spring borer activity is resumed, they should be decked in the shade during the winter or early spring. This will lengthen the developmental period, thereby permitting more time to get the logs into water before beetle emergence occurs. Should conditions prevent the removal of the decks, the slower development of the borers under dense shade conditions will cause much of the beetle emergence to occur so late in the summer that their progeny will have a 2-year life cycle, thus materially reducing the protential rate of increase of the borer population.

Cutting practices

All silvicultural practices that tend to reduce weakening of the forest by exposure and drought also tend to control the borer population. Light selective logging has been adopted by the forestry department of the reservation as the best method of handling the hemlock type. Experimental cuttings conducted during the course of this investigation substantiate this choice.

Light selective logging.— To study the effect of exposure on the residual hemlock stand following logging, four 1-acre sample plots were established in the fall of 1939. Two of the plots were marked and logged in October 1939. The logging operation removed 9,845 and 7,280 board feet (gross volume) respectively from these plots. A third plot was established in a 10-acre experimental area that had been logged during the winter of 1938-1939 to remove as near 25 percent of the stand volume as possible. Thus, the logging operations removed 32, 29, and 25 percent of the respective gross volumes from these plots (table 9). A fourth plot, a check, was established in an adjoining block of virgin forest in which no logging will be done. Following the logging operations on plots 57 and 58, the hemlock slash was collected and the boughs used to mulch ¼ of the area of each plot.

Due to abnormally heavy precipitation and cloudy weather during the summer months of both 1940 and 1941, no significant results were obtained from the mulching. However, a re-examination of these plots in October 1941 showed considerable mortality due to blow-down. The majority of the blow-down damage had occurred during 1941. The more heavily thinned of the plots, No. 57, had 10 dead trees of which all but 1, a small 10-inch d.b.h. tree, had been either windthrown or knocked down by a windthrown tree. These trees had an aggregate volume of 2,015 board feet and represented 9.46 percent by volume of the green timber composing the residual stand after the 1939 logging operation. The mortality percentage for the other two thinned plots was 4.47 and 0.35. On these plots wind caused all the mortality on the first and a third of that on the second. The check plot had no mortality.

The present stand volume of plot 57, after deducting the 1939-41 mortality volume, is 19,274 board feet, because of the very dense original stand. This is greater than the residual stand volume of either plot 58 or 60 (table 9). However, the greater blow-down volume indicates that the trees of this plot are not as windfirm as those of the other plots. Therefore, even in a very dense stand the removal of 32 percent by volume was too heavy a cut to make in one operation in a hemlock type stand. In recent years, by the use of truck transportation, the forestry department of the Menominee Indian Reservation has found that it is economically possible to cut selectively as little as 4,000 board feet per acre. The above study substantiates this practice of light cutting and indicates that in a nearly pure hemlock type a cut of not more than 20 to 25 percent of the stand volume is advisable. These percentages mean a cut of about 6,000 board feet in stands of 30,000 board feet per acre and about 4,000 in stands of 16,000 to 20,000 board feet of merchantable size timber.

Table 9
1939-41 Tree mortality of
the exposure study plots

Plot No.	Original volume (gross) bd. ft.	Volume removed by logging bd. ft.	Percent thinned by volume	1939 residual stand volume	1939-41 Tree mortality No. trees	1939-41 Tree mortality Gross volume bd. ft.	Percent residual stand volume
57	31,134	9,845	32	21,289	10	2,015	9.46
58	25,387	7,280	29	18,107	2	810	4.47
60	22,800	5,700	25	17,096	3	60	0.35
59	35,301	0	0	35,301	0	0	0 (Check plot)

Selective group cutting.--In general, the selective logging on the reservation has been made by individual tree selection. In stands

where there is an uneven age condition, this method works very well and has the advantage of not making any large holes in the forest canopy. However, occasionally overmature hemlock stands of relatively even age class are found. Plot 7, discussed on page 66, is in a stand of this type. On this plot the logging of 17 percent of the volume, in a stand averaging about 31,000 board feet per acre, would normally have been the proper cut. However, due to drought and the overmaturity of the trees, 47 percent of the residual stand died. This and similar instances observed during the years spent on the reservation have convinced the writer that a group selection rather than an individual tree selection method should be used in logging stands of this type. Such a method will have a minimum disturbing effect on the residual stand, and although exposure may eventually kill the trees bordering the cut areas, they too can be salvaged with little disturbance to the majority of the stand.

Where 8 or 12 overmature hemlocks are growing together as a group, frequently after the cutting of one or two the others soon die. In stands where the greater part of the volume was composed of groups of this type, any appreciable cutting of scattered trees started the decadence of so many groups that the subsequent salvage operations resulted in nearly clear cutting. Thus, in such areas it appears best to cut lightly using a group selection method. This would mean cutting the weakest group in each acre, leaving wherever possible hardwoods or young hemlocks bordering the opening, then moving on to the next acre before taking another group of 8 or 12 trees.

This group selection method of cutting hemlock is not entirely an original idea of the writer's. It resulted more from observing that in the salvaging of overmature stands, a group type of cutting took place.

It was also noted that in virgin stands of similar age class the tree mortality was generally much less than in the stands that had been logged. Thus, in collaboration with Supervisor Delaney, it was agreed that a group method of marking should have merit since it would follow nature's trend and leave more groups in a virgin stand condition until more favorable climatic conditions permitted their removal. Subsequent testing of this method in several areas gave favorable results.

SUMMARY

The beetle has a black metallic colored body of typical buprestid shape. Its average length and width is 10 mm. by 4 mm. Each wing cover is commonly, though not necessarily, marked with 1 to 4 yellowish- or orange-colored spots.

The hemlock borer may have either a 1-year or a 2-year life cycle depending on the condition of the cambium of the host and the time at which oviposition occurred. The life cycle is 1 year for early summer ovipositions on material that provides a favorable environment, and 2 years for late summer (August) ovipositions on similar material. Under less favorable environmental conditions July ovipositions may have a 2-year cycle although the 1-year cycle is the rule.

The incubation period for the egg is usually a week.

Temperature has a noticeable effect on the length of the larval and pupal periods. The peaks of beetle emergence from infested logs decked in the shade was 2 to 4 weeks later than that for similar logs decked in the open.

The lethal temperature for hemlock borer larvae was not determined, but evidence was found indicating that they can resist rather high subcortical temperatures. Some larvae survived temperatures of 110° F. In the log deck studies of 1939, larvae developed to maturity in the cambium of the upper quadrant of large diameter logs that were exposed to direct sunlight throughout that summer. In contrast, on stems of 10-inch diameter there was practically a total killing of the borers in the exposed quadrant.

The maximum length of life for the beetles under caged conditions was 19 days. The probable length of life of "free" beetles is 1 to 2 weeks.

The beetle flight in this region normally begins about June 1 and extends through August. During the unusually early spring of 1939, the flight began between May 18 and 22.

The behavior of ovipositing beetles is controlled by certain tropisms, chiefly those relating to temperature and light. Observations showed that 80 percent of the ovipositions occurred when the air temperature at the bark surface was between 82° and 92° F., with the optimum at about 86° F.

A count of the eggs and oocytes of 30 gravid females showed a biotic potential range of 100 to 160 eggs per beetle.

The sex ratio is approximately one to one. A study of the sex ratio in the daily beetle migration to the trees to oviposit showed that both sexes were equally represented.

A number of characters commonly associated with a hemlock borer infestation were found. These were woodpecker work, the root rotting fungus (Armillaria mellea (Vahl.) Quel.), and four crown and stem characters. Three of the last five characters were apparent before a successful borer infestation actually developed. They were a reliable criterion for detecting dying hemlock as early as 2 years prior to complete shattering of the needles.

Borer attacks on the half-girdled trees were not successful until several years following the girdling, when the trees were in a dying condition. The check trees were never successfully attacked. This shows that the borer is a secondary insect.

The girdled tree series and the root examination studies showed that normally hemlock does not shatter all of its needles until 2 to 3 years following fatal injury.

Twenty-eight large hemlock trees were selected because of various stages of hemlock borer infestation and their root systems exposed and examined. These examinations definitely showed that the trees had to be in a dying condition before the borer could attack and successfully develop in them. Successful attacks were found only on trees with 52 percent or less of their main lateral roots alive. These trees had practically no living root caps and only 2 to 10 percent of the small feeder rootlets were living. Galleries of unsuccessful attacks that etched the wood were prevalent, but no galleries of successful attacks were found in trees having 60 to 83 percent of their main lateral root systems alive. These usually had less than 60 percent of their root tips alive. The check trees had about 98 to 100 percent of their main lateral roots alive and the majority of their root tips were living.

An examination of the annual rings showed that the successfully attacked trees usually failed to lay on wood at the lower part of their bole 1 to 2 years prior to the beginning of successful attack. This indicated conclusively that the trees were in a weak and decadent condition before successful attack occurred.

For the period 1925-1940, a good correlation was found between precipitation and tree growth. A close correlation was found between the current year's hemlock growth and a precipitation departure value, obtained by combining the departure (from the average) of the preceding year's growing season with the departure of the current year's spring season. For certain years, a closer correlation was found between tree growth and a

precipitation value obtained by combining the precipitation departures (from their respective averages) of the preceding year's growing season, the current year's spring season, and the current season's 12-month October-September period. It was found that a summation or mean precipitation value based on the precipitation of both the current and preceding years will give a better correlation with the current year's hemlock growth than either season's precipitation taken separately.

The winter larval mortality of the borer does not normally exceed 10 percent.

Seven parasites of the hemlock borer were found. Four of these were new, undescribed species. Biological data were taken for these species. The highest parasitization in the areas examined was 50 percent. It is doubtful if parasites will ever prove a satisfactory control factor for the hemlock borer.

Woodpeckers are the most important of the predators. Ants are second in importance. However, as a control factor predators are not as effective as parasites.

Climatological phenomena, such as drought, heat, and high winds, were observed to have primary influence on the hemlock borer population. An examination of 67 sample plots clearly showed that unfavorable climatological conditions during 1931-37 were the principal factors responsible for the heavy hemlock mortality of 25 percent by volume that occurred on the Menominee Indian Reservation during the decade 1931-40 and resulted in the building up of an epidemic hemlock borer population in 1936-39.

In open stands, produced by former blow-down injury, heat and exposure were the principal factors responsible for a doubling in the

hemlock mortality rate during 1937-40.

Through their effect on the host trees, the site factors, such as soil and stand density, indirectly affect borer abundance. The majority of the hemlock stands were on light soil types having a low water holding capacity. Therefore, they were very susceptible to drought injury.

An area, which had 40 percent of its volume removed by a logging operation just prior to 1929, had a mortality of 50 percent of the residual stand volume in 1929 and 1930. This shows that in a hemlock type stand a heavy mortality from heat and exposure will follow if a heavy logging operation is made. In contrast, the mortality during the same period in a dense virgin stand on an adjoining area was only 9 percent by volume.

Since the hemlock borer has been shown to be definitely a secondary insect, direct control measures are not necessary or economically justified.

Certain practices may be followed which have a control value yet are economically sound because they also constitute good forestry practice in handling mature hemlock type stands. These are: (1) the use of the criterion developed for identifying dying hemlocks in the marking of timber; (2) the winter decking of infested logs in the shade when it is necessary to leave them in the woods until after spring borer activity is resumed; (3) the light selective logging of uneven aged stands; (4) the group selective logging of overmature even aged stands.

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Figure 1.--Heavy hemlock mortality occurred on the Menominee Indian Reservation between 1934 and 1939. The dead and dying trees were usually found to be infested by the hemlock borer.

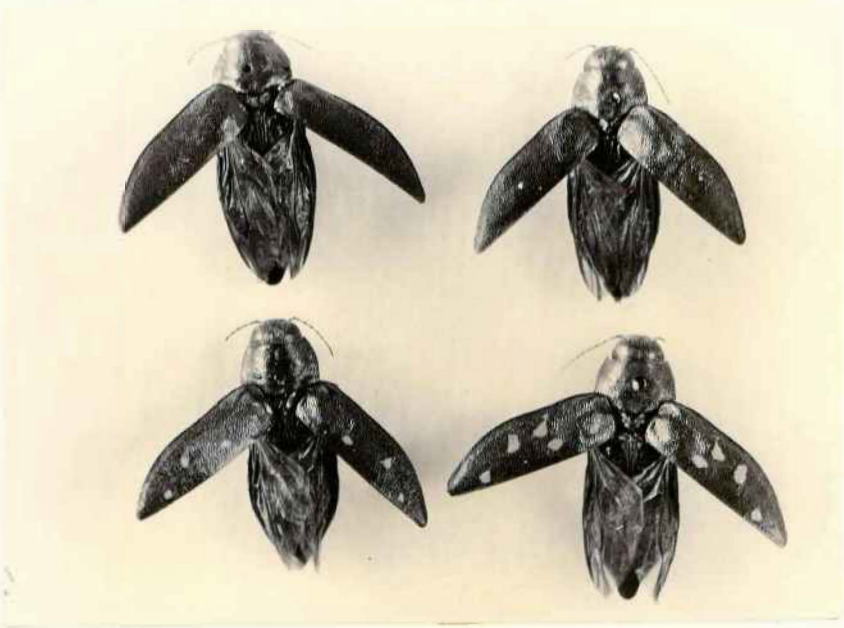


Figure 2.--The number of spots on the wing cover may vary from none to four. The above beetles, left to right, have none, one, three, and four spots per elytron respectively. Enlarged 3X.

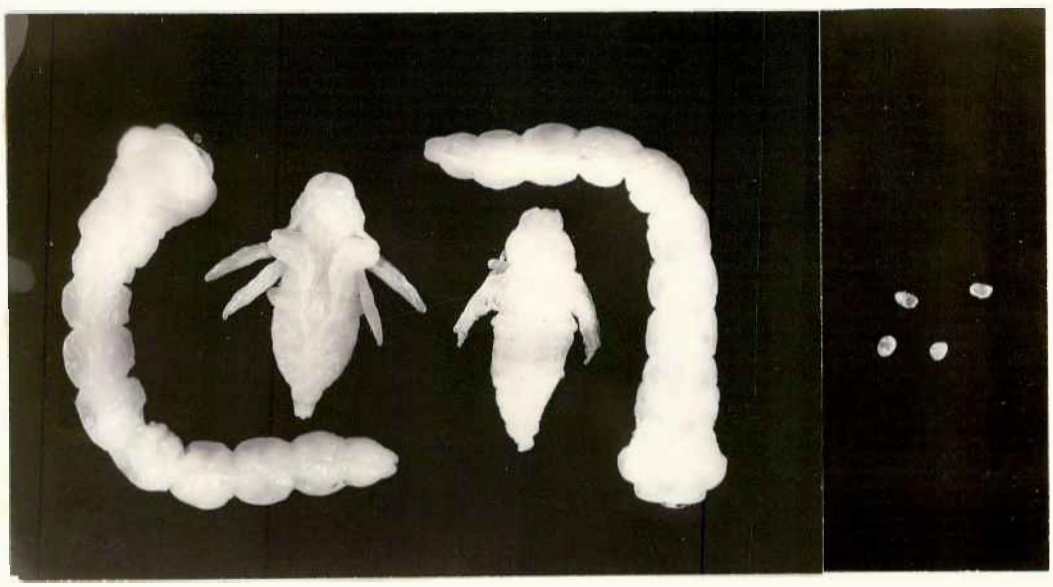
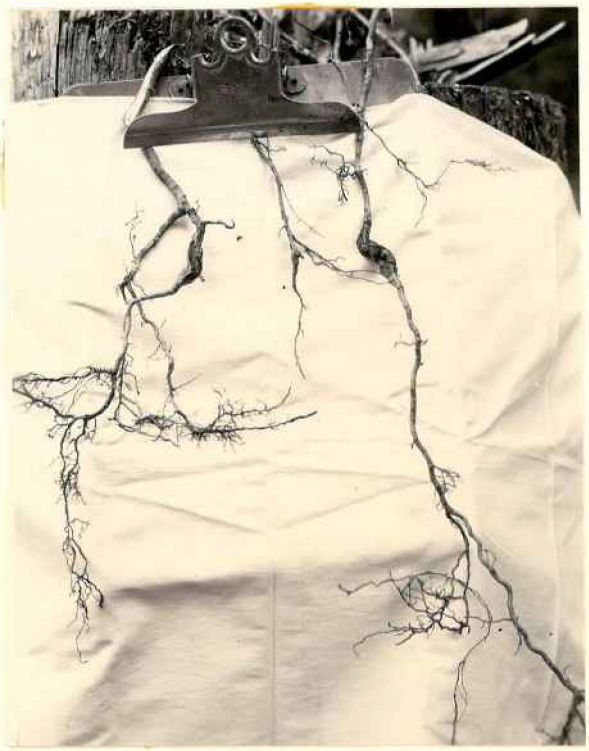


Figure 3.--Larvae, pupae, and eggs of the hemlock borer, X 3.

Figure 4.--Sporophores of *A. mellea*.



A

B

Figure 5.--A, Armillaria mellea cankers were common on both the main and small roots of the drought injured hemlocks; B, often the roots were rotted off at old cankered points.

Figure 6.--The thinning of the foliage, particularly at the terminal portions of the branches in the upper crown, is usually the first external indicator of hemlock decadence. This can be detected 2 years prior to complete needle fall. Tree 45, on the right, shows the crown condition about 1 year prior to complete needle fall. The tree at the left shows light injury from drought, but it will recover.

Figure 7.--Three hemlocks with crowns that are typical of a vigorous healthy tree (left), a dead tree (center), and a dying tree (right).

Figure 8.—When present in numbers, the feeding of the larvae may cause a girdling of the cambium tissue of the tree trunk.

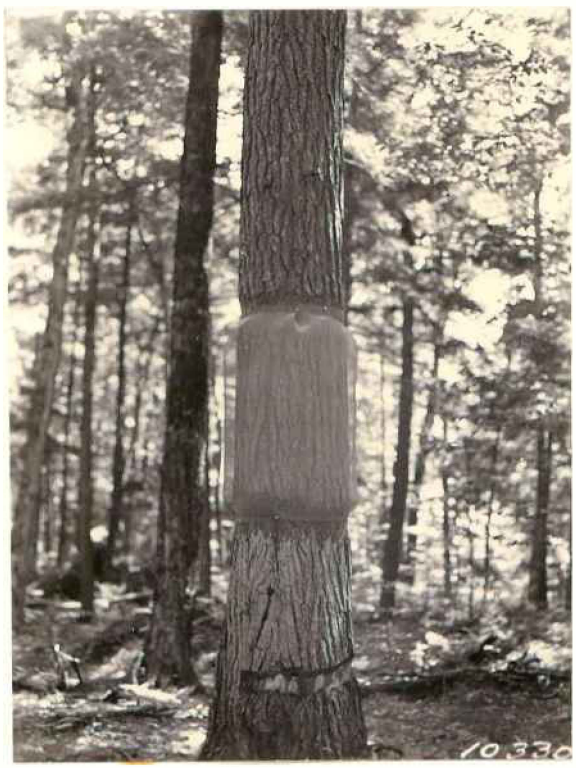


Figure 9.--A series of trees were half-stem-girdled in the spring of 1938 to study their resistance to caged borer attacks.

Figure 10.--Frequently on trees that still retained 75 percent of their foliage and had little or no successful borer attack, barking of the lateral roots at soil level showed the root system to be entirely dead and mycelial fans of Armillaria mellea present on most of the main lateral roots.

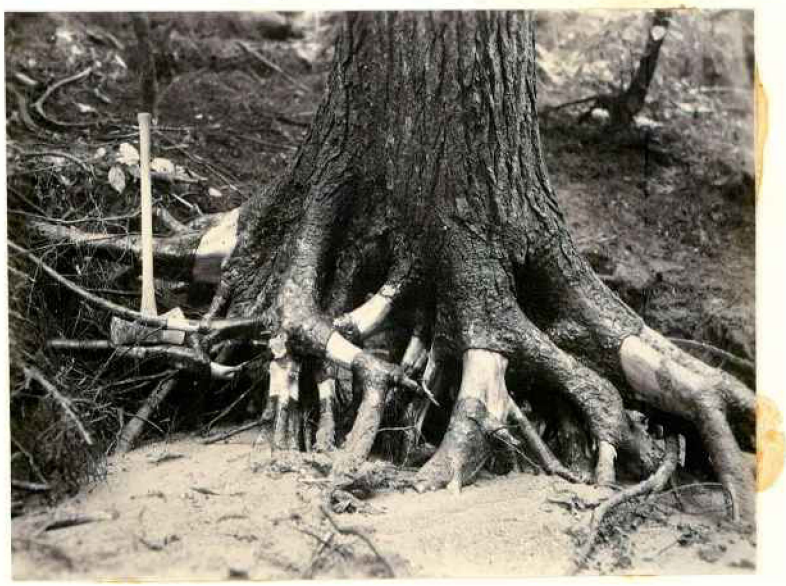


Figure 11.--To determine how long trees with dead root systems will retain their foliage, the root collars of several trees were washed out, the roots girdled, and the soil washed in again to its original level.

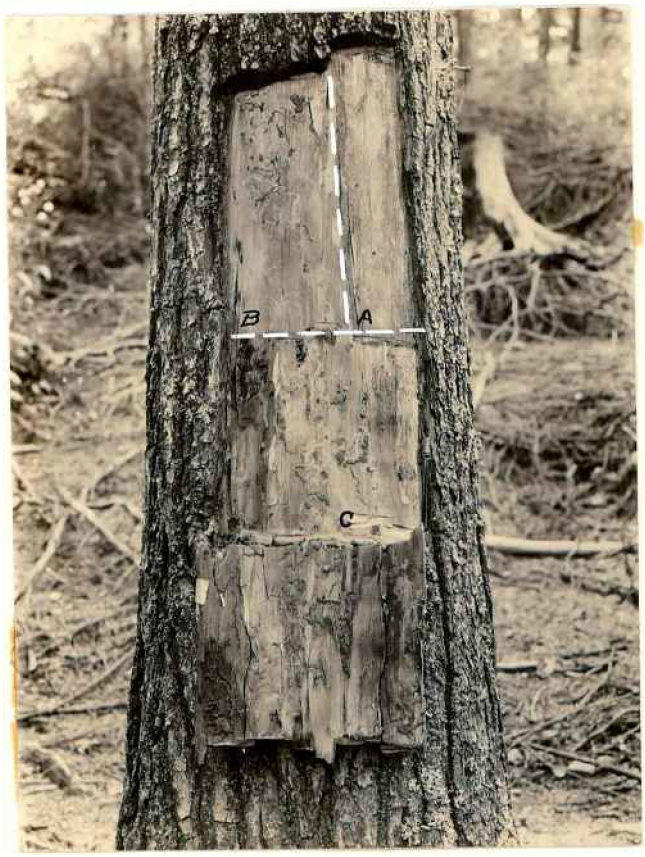


Figure 12.--The 100 percent root-girdled trees contained no borer infestation when treated in August 1939, see area A. In August 1940 they had a heavy larval population (area B), the majority of which were mature by October 1940 (area C). The arrow on the bark from area C indicates where a mature larva entered the bark to pupate while farther to the left two larvae, one mature and the other nearly mature, are pinned beside their respective galleries.

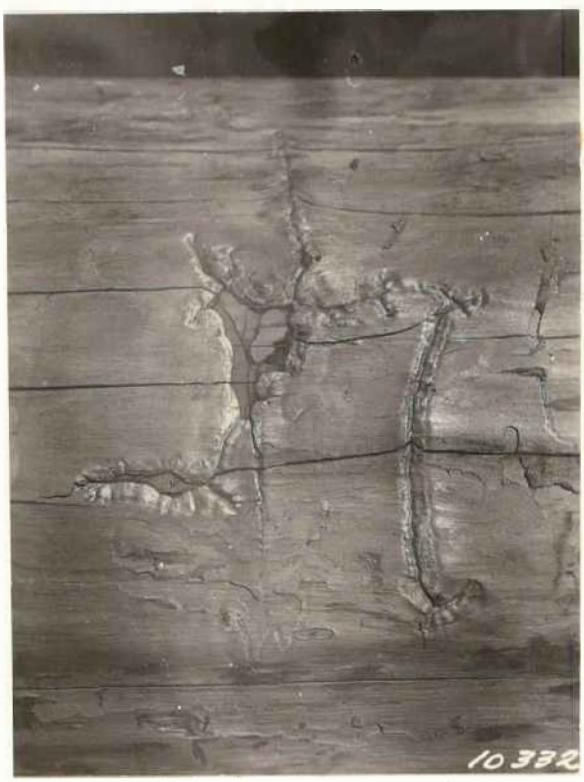
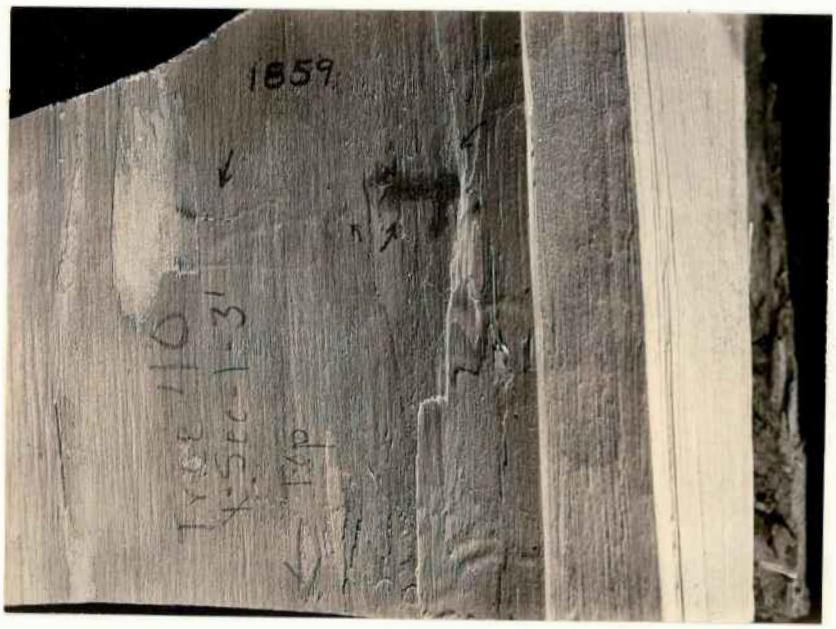


Figure 13.—Callous tissue formation over an old unsuccessful attack. Shows borer galleries etched in wood laid on in 1934. The tree on which this scar was found died during 1938. Examined August 1938.

A



B

Figure 14.—A, A cross section of hemlock in which the arrow indicates an unsuccessful attack gallery made in 1938. B, A longitudinal section showing initial unsuccessful borer attack galleries in wood laid on in 1859. This section split readily along the 1859 annual ring.

Figure 15.—Hemlocks of the root condition study. The shovel to the right of the stump in the foreground shows the vertical depth of the excavation to be about 6 feet below the original ground level. Some roots were examined to a length of 27 feet.

Figure 16.—During 1939 and 1940 the root systems of 30 trees representing various stages of hemlock borer attack were washed out and examined.

Figure 17.—An examination of the roots definitely showed that drought was the primary cause of the tree mortality. The majority of the small rootlets were dead and rotted off, leaving only the larger roots which were studded with root stubs.

Figure 18.--Hemlock has a very shallow root system. An excavation 6 feet deep usually exposed most of the vertical root system.

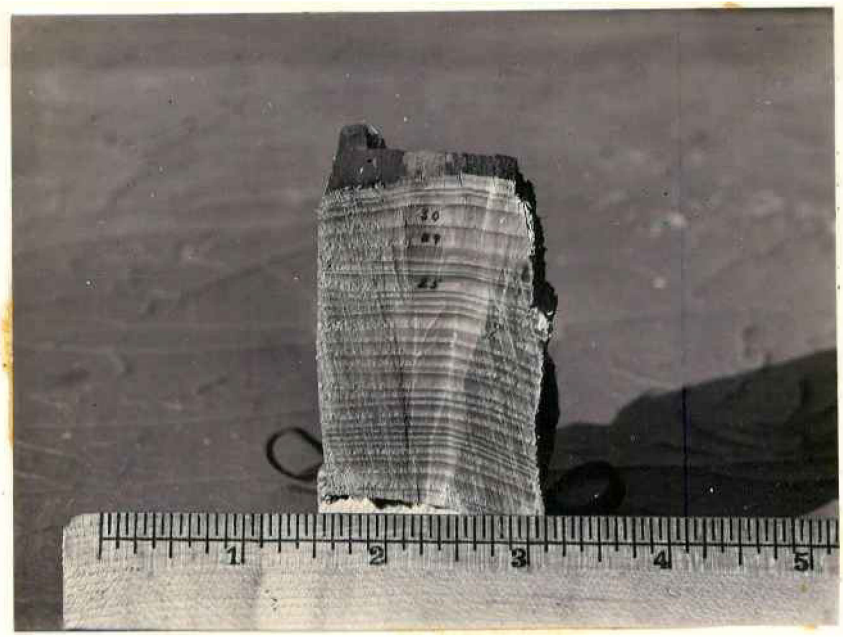


Figure 19.--Certain combinations of wide and narrow rings, which were present on practically all hemlocks, made a ring pattern that was easily cross identified between trees. This block, from the base of a tree that dropped its foliage in the spring of 1938, shows 1935 to be the last year that wood was laid on the lower bole.

Figure 20.--Stagheaded yellow birches and hemlocks were common following the 1930-37 drought.

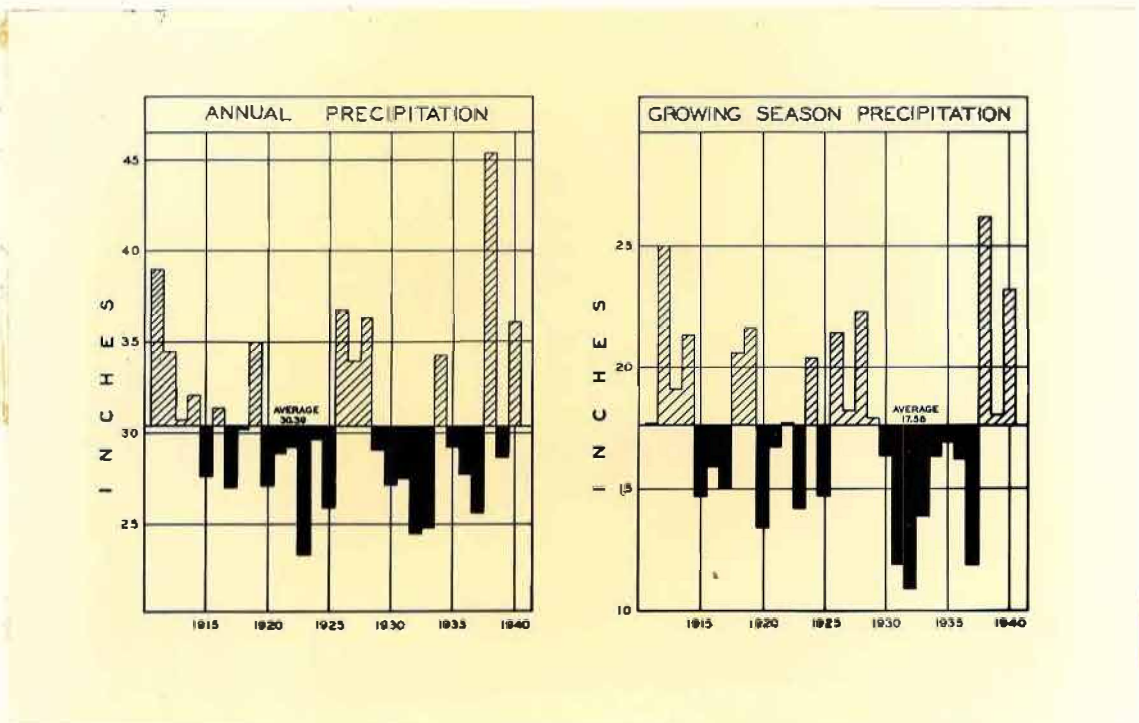


Figure 21.--The precipitation departures from the average at Antigo and Wausau during the 30 year period, 1911 to 1940.

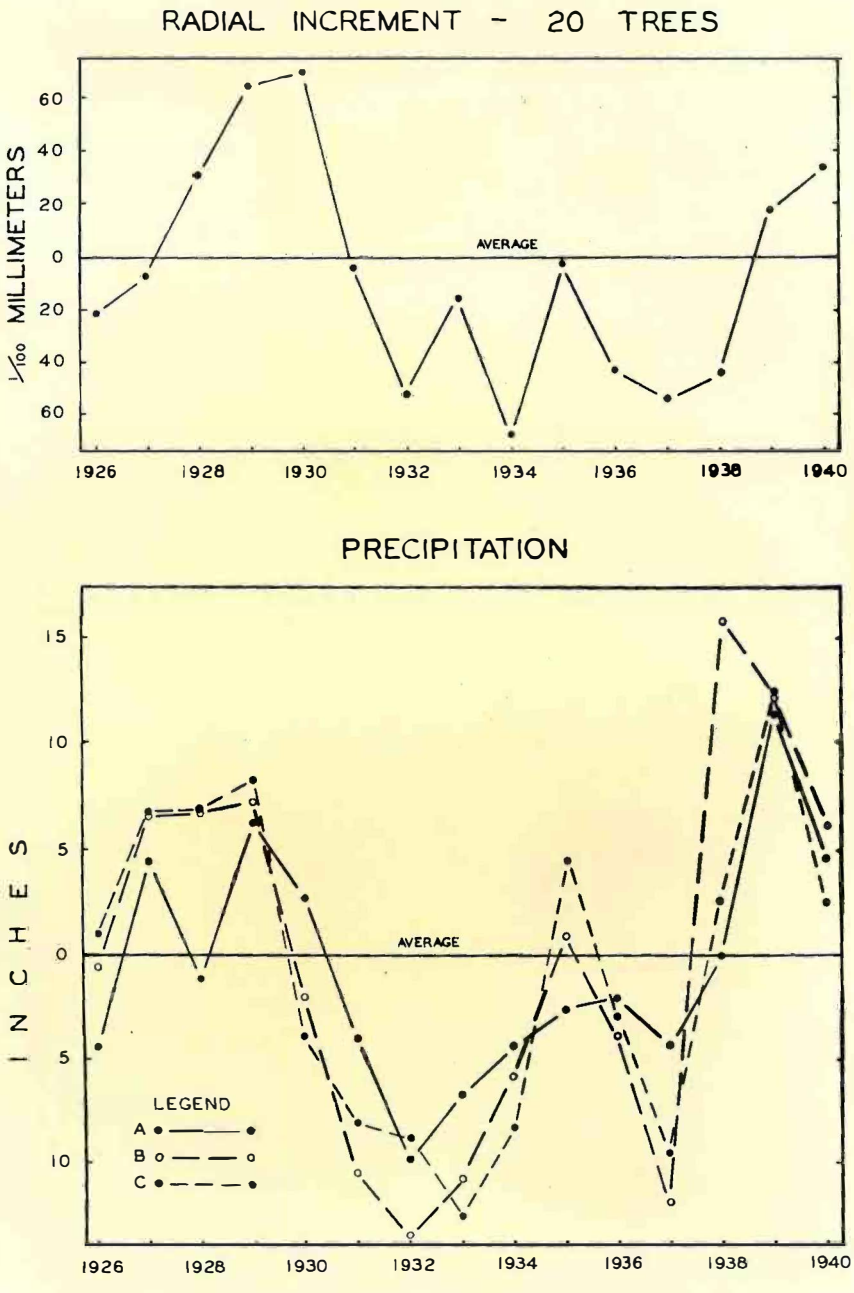
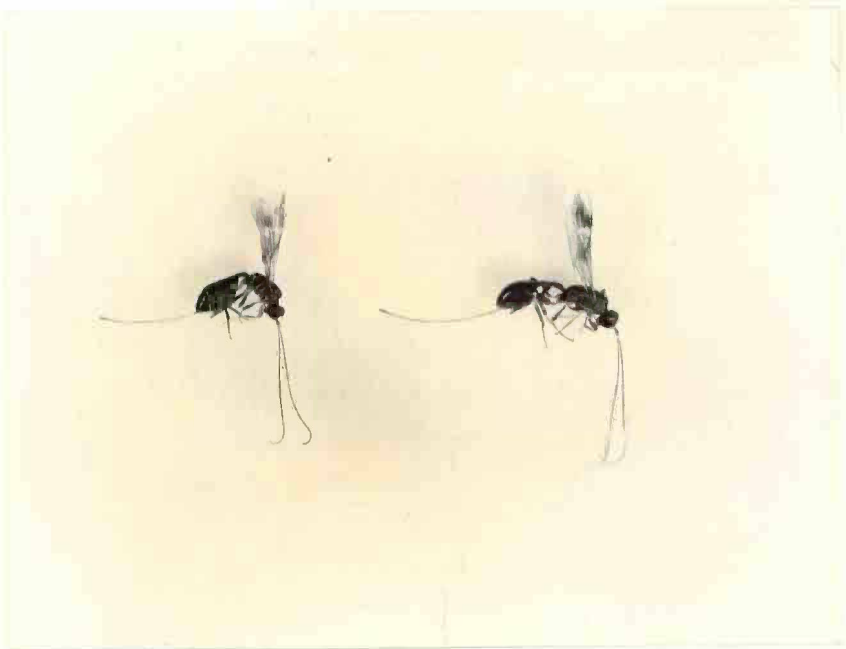


Figure 22.--A correlation was found between precipitation and radial increment. The 3 graphs of the precipitation chart are based on the departures of columns A, B, and C of table 5.

A

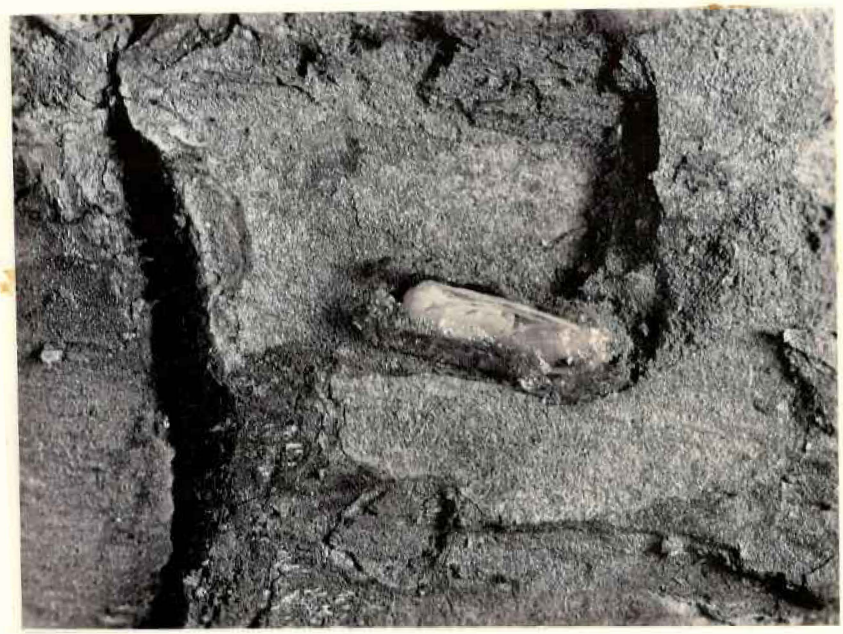
B



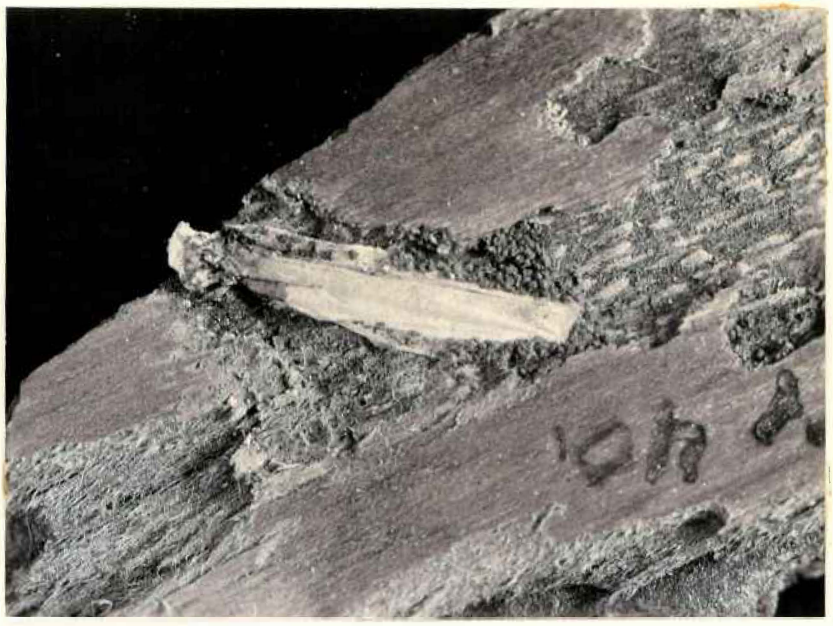
C

D

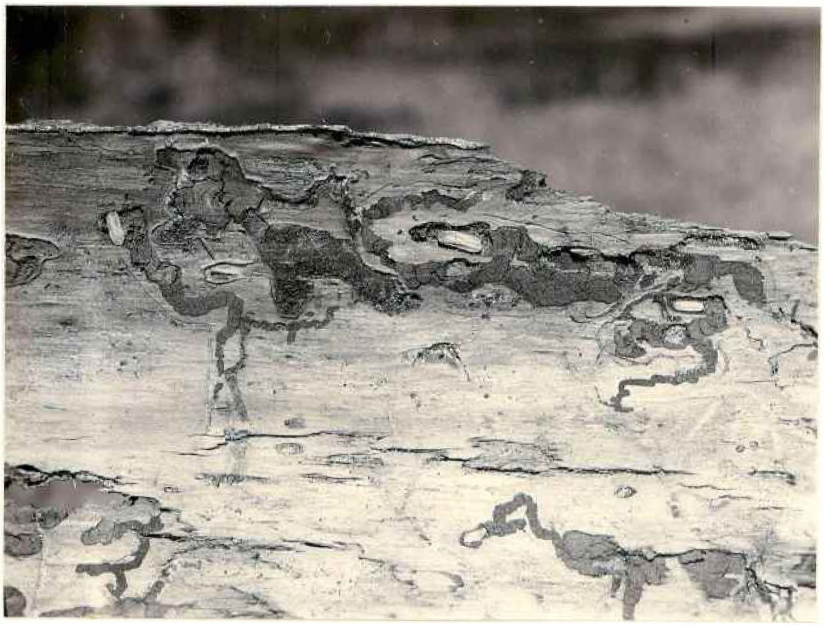
Figure 23.--Parasites of the hemlock borer: A, Atanycolus n. sp., X 4; B, Odontaulacus bilobatus (Prov.), X 3; C, Spathius n. sp., X 4; D, Ichneumon n. sp., X 2.



A



B



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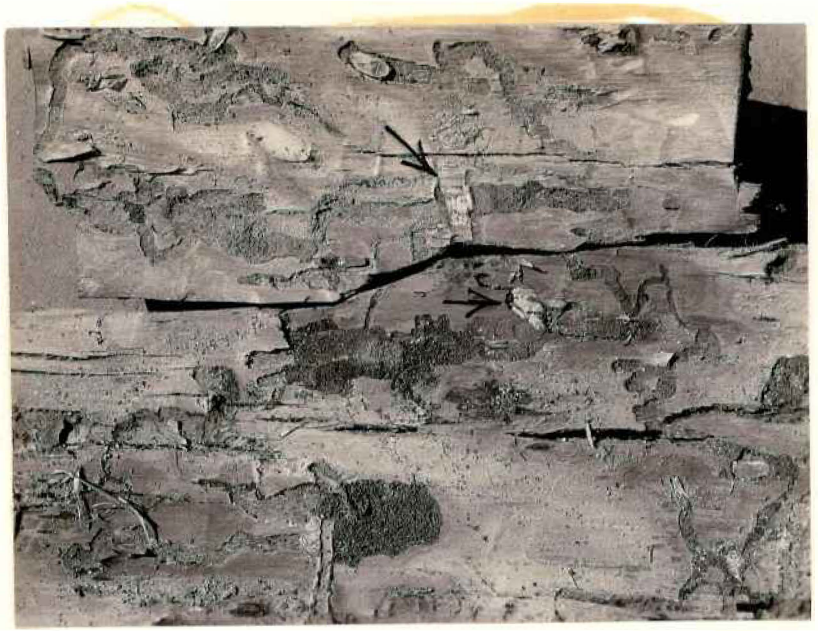

D

Figure 24.—Cocoons of hemlock borer parasites: A, Odontaulacus bilobatus (Prov.), X 2.6; B, Ichneumon n. sp., X 3; C, Atanycolus n. sp., X 0.6; D, Spathius n. sp., X 0.5.